

# No. 5 — *Triassic Reptile Footprint Faunules from Milford, New Jersey*

By DONALD BAIRD

## CONTENTS

	Page
FOREWORD	449
GEOLOGICAL OCCURRENCE	451
SYSTEMATIC DESCRIPTIONS	452
THEROPODA	
<i>Grallator sulcatus</i> Baird, n. sp.	453
<i>Anchisauripus milfordensis</i> (Bock)	462
<i>Anchisauripus parallelus</i> (Hitchcock)	464
Genus incertum	465
Taxonomy of theropod footprints	467
PSEUDOSUCHIA	
<i>Chirotherium parvum</i> (C. H. Hitchcock)	473
<i>Chirotherium eyermani</i> Baird, n. sp.	479
PHYTOSAURIA	
<i>Apatopus lineatus</i> (Bock), n. gen.	486
LACERTOIDEA INCERTAE SEDIS	
<i>Rhynchosauroides hyperbates</i> Baird, n. sp.	494
<i>Rhynchosauroides</i> sp.	497
CORRELATIVE AGE OF THE MILFORD FAUNULES	501
REPTILES OF THE BRUNSWICK FORMATION	503
APPENDIX I: The nature of <i>Otouphepus</i>	507
APPENDIX II: <i>Brontozoum</i>	509
SUMMARY	511
REFERENCES	514

## FOREWORD

In a recent paper Wilhelm Bock (1952) has described a number of important faunules of fossil footprints from various horizons and localities in the Upper Triassic (Middle Keuper) of the Newark Basin. One of these faunules, found in a gray sandstone layer of the upper Brunswick formation near Milford, New Jersey, had been discussed in the literature as early as 1886; but until 1952 only its dominant species, *Chirotherium parvum*, had been adequately described. In the same paper

Bock described a new species of pseudosuchian footprints, *Chirotherium lulli*, found in a reddish-brown siltstone bed at the same locality. More recently a slab bearing the counterpart trackway of *C. lulli* and two forms of dinosaur tracks has come to light and, with Bock's generous permission, has been described (Baird, 1954).

Most of the Milford footprints discussed by Bock had been collected by John Eyerman in 1885 and deposited in the geological museum of Lafayette College at Easton, Pennsylvania (hereafter abbreviated LC). One slab, privately owned, had been acquired by Bock for the Academy of Natural Sciences of Philadelphia (ANS). While Bock's paper was in press, Eyerman's second and much larger collection from the same quarries came to light in the Museum of Comparative Zoology (MCZ), and received independent preliminary study. This material, though described in part by Eyerman in 1889, had been overlooked by subsequent authors. A search of the American Museum of Natural History collections (AMNH) has produced eight additional footprint-bearing slabs collected at Milford by Eyerman in 1886.

Besides increasing the *Chirotherium parvum* faunule by several species and permitting morphological re-interpretation of those already described, the additional material includes a new species of dinosaur footprint which represents a third Milford faunal horizon. As this material also explains certain 19th-century misidentifications which have distorted the faunal picture, and the geological correlations which have been based on it, I have undertaken a comprehensive re-examination of the Milford reptile footprints and their zoological and stratigraphic significance.

I am particularly indebted to Wilhelm Bock for photographs and for permission to mold the type of *Chirotherium copei*, to J. L. Dyson for the loan of the Lafayette College types, and to E. H. Colbert for the loan of American Museum specimens and for generously making available his unpublished data on *Coelophysys*. Special thanks for the privilege of studying the collections under their care are due to G. W. Bain, A. E. Wood, and R. E. Schortmann at Amherst, R. G. Chaffee at Dartmouth, E. H. Colbert and Mrs. R. H. Nichols at the American Museum, D. H. Dunkle at the U. S. National Museum, J. T. Gregory at Yale, J. L. Kay at the Carnegie Museum, and C. W. Waldron,

Jr. at the Museum of Science, Boston. For their helpful and stimulating suggestions I am pleasantly indebted to C. L. Camp, E. H. Colbert, the late R. S. Lull, the late J. H. McGregor, F. E. Peabody, and D. M. S. Watson. The continued support and encouragement of Dr. Alfred S. Romer, as well as his critical reading of the manuscript, are most gratefully acknowledged.

## GEOLOGICAL OCCURRENCE

Two distinct footprint horizons bearing mutually exclusive faunules occur in the gray sandstones of the Milford quarries. Eyerman nowhere indicates the relative stratigraphic positions of these horizons, but they are probably not very widely separated: both are referred to the upper Brunswick formation, about 5,100 meters above the Triassic base. For clarity they are here arbitrarily designated Levels A and B. Although this cannot be stated as certain, Eyerman's discussion of the MCZ material (1889, p. 32) implies that the Smith Clark quarry was the source of the Level B or *Chirotherium parvum* faunule, while another quarry about one-half mile to the east furnished all the material from Level A.

At Level A, the footprints were impressed in gray shale and are preserved as natural casts on the under surface of a gray sandstone 4 to 6 cm. thick. The upper surface of this sandstone is irregularly excavated into shallow pockets in which adhere pieces of the overlying gray shale. All the footprints are referred to a single species, *Grallator sulcatus*. Most are deeply impressed, between 1 and 2 cm. below surface level at their deepest points; many are obscured by slippage, overlapping, or slumping of the extruded clay. None shows impressions of the plantar scales and very few show fringe-scale striations. Among the tracks on MCZ 216 is a striated drag-mark 25 mm. wide by 2 mm. deep, flanked on either side by intermittent shallow scratches. This might be interpreted as a tail-trace but is more probably the drag-mark of a Triassic conifer or horsetail rush. Very similar marks in the *Chirotherium* sandstone of Thüringen have been described as drag-marks of *Equisetites* by Rühle von Lillienstern (1939, p. 370, pl. 12). Narrow shrinkage cracks, rarely more than 5 mm. wide, characterize Level A.

Level B, which carries the larger faunule, somewhat resembles A in lithology. The sandstone overlying the recording surface, however, quarries out in layered flagstones 1.5 to 3.5 cm. thick; the flat upper surfaces typically bear shallow ripples and run-off marks. Shrinkage cracks of variable width are common. Rain-drops have pitted both ground surface and footprints, obscuring the plantar surfaces; but the sides of several deeper tracks show striated claw-marks and fringe-scale furrows. Certain parallel series of sharp, shallow scratches may be of arthropod origin, but no trackway sequences are preserved. Annelids have perforated the layers after deposition; their sand-filled burrows loop down into the shale or course along the sandstone-shale interface, looking superficially like dasycladacean algae. To the Milford flora recorded by Bock (1952, 1952 A) may be added the genus *Necocalamites* (MCZ 211). Several slabs bear branching or reticular patches, presumably algal.

The third Milford footprint horizon, discussed in my previous paper (1954), lies in a reddish-brown siltstone which crops out in the Smith Clark quarry some 15 meters above Level B. Reptile footprints of pseudosuchian appearance occur at another horizon in that quarry but are unfortunately too vague and fragmentary for adequate characterization (see Bock, 1952, pl 49, fig. 8).

The stratigraphic correlation of these beds with those of southeastern Pennsylvania, the Connecticut Valley, and central Europe will be discussed after an analysis of the fauna.

### SYSTEMATIC DESCRIPTIONS

Nineteenth-century publications on the Milford footprints are so vague, confused, and contradictory that little faith can be placed in them. The foundations of Triassic ichnology had been so monumentally laid by Edward Hitchcock that footprints from any part of the Newark series were customarily identified by reference to Hitchcock's figures of species from the Connecticut River Valley. This practice led inevitably to confusion, for the classic Connecticut Valley faunas actually have little in common with those of Pennsylvania and New Jersey. As the nomenclature of Triassic footprints evolved, faunal revisers changed the names of Milford species without checking the determina-



tions. For brevity, the terminologies of earlier authors and of this paper are summarized in Table 1.

Before Bock's restudy, only C. H. Hitchcock (1889) had erected new species for Milford footprints. His descriptions, unaccompanied by figures, are so vague that of the species mentioned only one, *Chirotherium* ["*Otozoum*"] *parvum*, can be identified positively. His new species "*Chimaerichnus ingens*," characterized only as "two relief tracks of considerable size and representing only one-half of the foot," is a nomen nudum. Any nomenclatural questions arising from C. H. Hitchcock's work have, fortunately, been settled by Bock's designation of types.

## Order SAURISCHIA

### Suborder THEROPODA

#### Infraorder COELUROSAURIA

Form-family GRALLATORIDAE Lull, 1904

(=ANCHISAURIPODIDAE Lull, 1904)

Genus GRALLATOR E. Hitchcock, 1858

Type species *G. cursorius* E. Hitchcock (1858, p. 72) designated by Lull (1904, p. 494).

GRALLATOR SULCATUS Baird, n. sp.

Figure 1; Plate 1, figure 1.

*Type.* MCZ 215, a left pes imprint.

*Hypodigm.* MCZ 215-228 inclusive, slabs bearing 37 pes imprints; AMNH 1982 and 1983, 6 imprints; LC S487, parts of 3 overlapping imprints. All collected by John Eyerman, 1885-1887.

*Horizon.* Upper Triassic (Middle Keuper), Newark series, upper Brunswick formation. Level A.

*Locality* (*fide* Eyerman, 1889, p. 32). Quarry of the Messrs. Clark about one-half mile east of the Smith Clark quarry, near Milford, Hunterdon County, New Jersey.

TABLE 1: ATTEMPTED SYNONYMY OF MILFORD FOOTPRINTS

Dashes indicate derivation from a previous author.

EYERMAN, 1886	C. H. HITCHCOCK, 1889	EYERMAN, 1889
LEVEL A:		
aff. <i>Anomoepus major</i>		<i>Brontozoum isodactylum</i> <i>Grallator cuneatus</i>
	[?] <i>Grallator parallelus</i> —————	
	[?] <i>Grallator cuneatus</i> —————	
LEVEL B:		
	[?] <i>Grallator cuneatus</i>	
	[?] <i>Grallator gracilis</i> —————	
		[?] <i>Grallator tenuis</i>
aff. <i>Anomoepus major</i>	<i>Otozoum parvum</i> , n. sp.	
		<i>Anomoepus minor</i> —
	[?] <i>Chimaerichnus ingens</i> , n. sp. —————	
	[?] <i>Polemarchus gigas</i> —————	
	<i>Argozoum dispari-digitatum</i> —————	

*Diagnosis.* A moderately large *Grallator*, differing from other species in the anterior position and relative shortness of digit III and in having the bases of II and III closely united, while IV is separated from III by a pronounced sulcus which extends back to the metatarso-phalangeal pad of III. Ovoid metatarso-phalangeal pads of II and IV regularly and equally impressing, that of II more anterior. Second phalangeal pad of II opposite first pad of III. Trackway characters unknown.

*Measurements.* Defects of impression and preservation make impossible a valid and consistent suite of measurements. Dimensions of the best-preserved specimens, however, suffice for descriptive if not for statistical treatment. Measurements of the type, adjusted for slippage and a transverse crack-filling, are as follows:

LULL, 1915	BOCK, 1952	BAIRD, 1957
Anchisauripus parallelus		} Grallator sulcatus, n.sp.
Grallator cuneatus — — —	Grallator	
	Gigandipus ? (Anchisauripus) milfordensis, n.sp.	} Anchisauripus milfordensis
Grallator gracilis — — —	Grallator gracilis	
		Anchisauripus parallelus
		Genus incertum
!Chirotherium parvum	Chirotherium parvum	} Chirotherium parvum
	Chirotherium copei, n.sp.	
		Chirotherium eyermani, n.sp.
	Otozoum (?) lineatus, n.sp.	} Apatopus lineatus, n.gen.
Sauropus barrattii — — —	Sauropus barrattii	
Sauropus ingens		
Polemarchus polemarchius		
Argoides macrodactylus — — — — —		(Unidentifiable)
		Rhynchosauroides hyperbates, n.sp.

Pes, digit no.	II	III	IV
Length, mm.	54	72	59
Length including metatarso-phalangeal pad	78	98	84
Length of pes, 100 mm.; including metatarso-phalangeal pads, 123 mm.; width, 60 mm.			

Measurements of digit divarication will vary greatly in a single footprint depending on one's reference points. In the type specimen the angles between axes drawn through the centers of claw base and metatarso-phalangeal pad are: II-7°-III-19°-IV. *Grallator sulcatus* footprints, however, show quite a range of divarication values. In my experience linear and angular measurements such as these have a very limited value for the diagnosis and differentiation of theropod footprints.

*Morphology.* The abundance of deeply-impressed footprints of this species affords an unusually clear picture of its foot structure, including the relationship of the distal ends of the metatarsals which is rarely recorded in *Grallator* trackways. As in other theropod dinosaurs and in most cursorial birds the

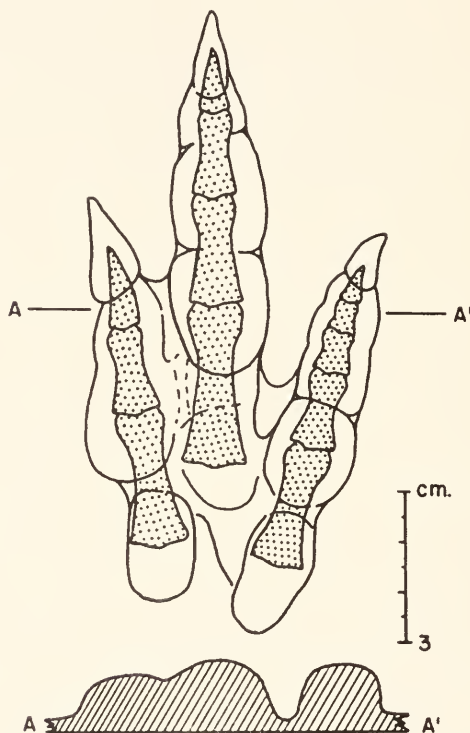


Fig. 1. *Grallator sulcatus* n. sp.,  $\times \frac{2}{3}$ . Composite outline based on the four best-preserved specimens. Section A-A' across the inverted natural cast shows the close association of digits II and III and the sulcus separating digit IV. Proximal phalanges of the restored skeleton appear foreshortened.

gait was digitigrade with most of the body weight falling on the joints between the first and second phalanges of digits II, III, and IV. Nevertheless, the pads which underlay the joints between metatarsals and phalanges of digits II and IV impressed

regularly, though less deeply than the digital pads, even in shallow imprints. Apparently this Brunswick species had not achieved the advanced degree of digitigrady shown by later inhabitants of the Connecticut Valley. Unfortunately the lack of trackway measurements precludes any useful comparison between gait patterns of Brunswick and Connecticut Valley *Grallatoridae*.

The claws of *Grallator sulcatus* are acuminate in some individuals but blunted by wear in others. Regardless of depth of impression the claws were always extended, rather than flexed as in the other Milford theropods; in particularly deep tracks the exaggerated depth of claw-marks is due not to flexure but to pivotal down-turning as the posterior part of the foot was raised.

The slightly domed phalangeal pads coalesce to form a sole callus which appears to have been slightly wider than the toe proper, as in many cursorial birds. The three metatarso-phalangeal pads, though they impressed less deeply, form an integral part of the sole and are separated from the phalangeal pads only by shallow sulci. The close union of digits II and III and the broad separation of IV differentiate *Grallator sulcatus* strikingly from its congeners, in which the digits are either laterally equidistant or III and IV are more closely appressed than II and III.

*Variation.* Footprints from Level A reveal a sobering degree of variability both in apparent form and in manner of impression. An increased divergence of the lateral toes is less common than an exaggerated out-turning of the claws alone. Whether this out-turning reflects some lateral flexibility at the ungual joint, or merely individual variation in the plane of a horizontally immobile joint, cannot be determined without trackways showing successive imprints of the same foot. Distorted deep impressions reveal that the lateral toes were spread apart as the foot sank into the mud and were contracted again in birdlike fashion as the foot was withdrawn.

Many of the footprints are so deformed by accidents of impression that they give a decidedly erroneous picture of the foot structure. Such anomalies serve to emphasize the dangers involved in any attempt to characterize and interpret footprint species without adequate quantities of well-preserved material.

A footprint is not an organism but the by-product of dynamic contact between an organism and its environment. The all-too-common typological analysis of isolated examples cannot be expected to yield zoologically significant information.

*Osteology.* Heilmann (1927, p. 179 ff.) and Peabody (1948, p. 399 ff.) have independently concluded that in the *Grallatoridae* the phalangeal pads must have underlain the joints. This is the situation in many cursorial birds, in which only the ungual joint may coincide with a transverse crease. The osteological restoration of *Grallator sulcatus* in Figure 1 conforms to this principle but differs enough from the examples cited by Heilmann and Peabody to require explanation. In my opinion the pes of *Procompsognathus* which Heilmann (1927, fig. 130 K) has superimposed on the footprint of *Grallator tenuis* would fit a great deal better if the foot were advanced until the ungual joints of digits II and III corresponded with the distal pads instead of their creases. All the joints would then line up neatly opposite pads, with both ends of the fourth phalanx of digit IV included in the distal pad. Except for the over-long claws of *Procompsognathus*, foot and footprint correspond well in structural pattern.

The otherwise convincing skeletal restoration of *Grallator cursorius* in Peabody's figure 37 B shows a crease coinciding with the joint between phalanges 3 and 4 of digit IV. Here again I would prefer to enclose both ends of phalanx 4 in the distal pad: and this is readily done if we use Hitchcock's original figure of the footprint (1858, pl. 13, fig. 3), in which the distal pad appears longer and more square-shouldered like that of *G. tenuis*. Other Triassic theropod footprints such as *Anchisauripus* and *Eubrontes* definitely have a long distal pad on digit IV, and an occasional median constriction of this pad suggests that two joints are actually represented. When the bones of any of these footprint types are restored on the plan advocated here, the phalangeal pattern is precisely that of Triassic and later theropods: the phalanges of digit IV are short, stout-shafted, and successively decreasing slightly in size.

No trace of a hallux is visible in any *Grallator sulcatus* footprint even where the metatarso-phalangeal pad of digit II is impressed as deeply as 14 mm. Obviously the hallux, while presumably present, was vestigial and completely non-functional.



The lengths of the proximal phalanges, usually indeterminate in more digitigrade coelurosaur footprints, can be estimated with fair accuracy from the positions of the regularly impressed metatarso-phalangeal pads. Pads II and IV are impressed to equal depths, differing only as one side of the footprint is deeper than the other. This situation contrasts sharply with that in other species of *Grallator* and in *Anchisauripus* and some species of *Eubrontes*, where the metatarso-phalangeal pad of digit II impresses less deeply or not at all. From this anomaly we may obtain some clue to the probable structure of the metatarsus.

If a Newarkian coelurosaur such as *Podokesaurus* is restored in a walking pose based on *Grallator* trackways (cf. Von Engel n and Caster, 1952, fig. 277), the metatarsus slants forward and downward at an angle of some  $115^{\circ}$  to the ground plane as the foot is implanted. As the metatarso-phalangeal pads were evidently developed to cushion the sole against the thrust transmitted down the metatarsus, and as they served this function only during implantation and the beginning of the propulsion phase, it follows that the position of their imprints is (broadly speaking) that of projections of the cross-sectional areas of their respective metatarsals when in the implantation position. If this be the case, as comparison with cursorial birds suggests, then the type of transverse arching of the metatarsal bundle at its distal end determines whether pad II or pad IV, or neither, makes the more posterior impression. Similarly, the relative length of the lateral metatarsals plus the thickness of their underlying pads determines the relative depth of the pad impressions. Of course the relative thickness of the pads is unknowable, but where the imprint of pad II is shallow or absent (as in most Newarkian theropod footprints) metatarsal II was probably shorter than IV. Conversely, the dinosaur represented by *Grallator sulcatus* appears to have had lateral metatarsals of approximately equal length.

Among Upper Triassic coelurosaurs metatarsal II is decidedly shorter than IV in *Procompsognathus*, but the lateral metatarsals are equal or subequal in *Ammosaurus*, *Halticosaurus* and *Coelophysis*. For comparison with *Grallator sulcatus* let us restore from their pedal skeletons the footprints that would have been made by two of these coelurosaurs.

*Halticosaurus liliensterni*, a massive species from the Knollenmergel of Thüringen, is described by Huene (1934) as having lengths of 20.5, 22, and 20 cm. for metatarsals II, III, and IV; digit I is unknown. To show the relative positions of the digits in walking pose we must make a three-dimensional reconstruction of the pes; when this is projected onto a horizontal plane

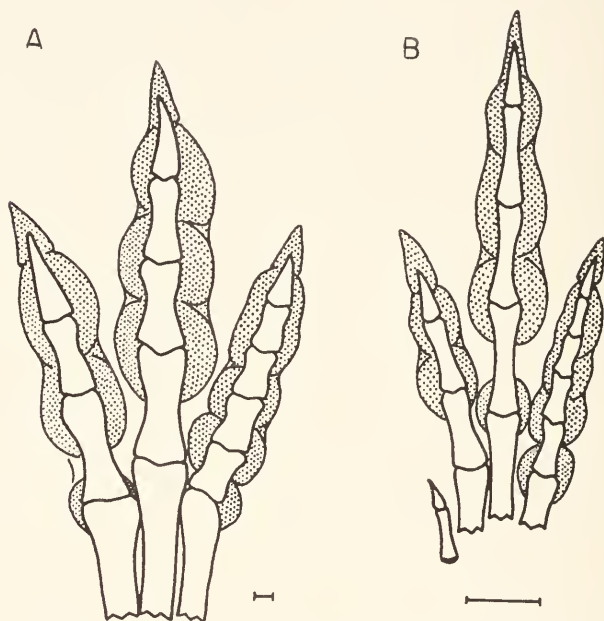


Fig. 2. Reconstructed right pedes of Keuper coelurosaurs, with restored footprints. A. *Halticosaurus*, x  $\frac{1}{4}$ . B. *Procompsognathus*, x 1. Data from Huene.

(analogous to a footprint-recording surface) the metatarsals and proximal phalanges are properly foreshortened (Figure 2 A). Structures in the metatarso-phalangeal region indicate a foot with a moderately compact base and strongly divergent digits; the bulk of the animal and the proportions of the metatarsus suggest that the posterior pads impressed regularly and to nearly equal depths. The positions of the plantar pads are deduced from the skeleton and a plausible reconstruction of their

original form can be derived from Connecticut Valley footprints of equivalent size.

The footprint thus restored is certainly neither a *Grallator* nor a *Gigandipus*, and apparently not an *Anchisauripus* sensu stricto. In *Eubrontes giganteus* and *Anchisauripus minusculus* we find the closest similarities in size, relative lengths of digits and phalanges, and regular and subequal imprints of the metatarso-phalangeal pads. Without venturing any positive correlation we can say that these footprints may well have been made by coelurosaurs of the *Halticosaurus* type.

*Procompsognathus triassicus* from the Stubensandstein of Württemberg is, in contrast to the hulking *Halticosaurus*, a graceful and diminutive species. When reconstructed (from Huene, 1921) and projected as before (Figure 2 B), its foot appears strikingly slender and laterally compressed. Neither the hallux nor metatarso-phalangeal pad II normally made contact with the ground. The restored footprint is obviously that of a *Grallator* closely comparable to a small *G. cursorius* but having a relatively shorter central digit. If the divarication were larger and the lateral digits somewhat shorter, correlation with a small *G. tenuis* would be indicated.

A comparison of Figures 1 and 2 shows clearly that, even disregarding size, *Grallator sulcatus* has much stronger resemblances to *Procompsognathus* than to *Halticosaurus*. So far as osteology can be inferred from the footprint, only size, minor differences in digital proportion, and the shortness of metatarsal II distinguish *Procompsognathus* from the Milford trackmaker.

Unpublished data on skeletons of *Coelophysis* from the Upper Triassic of New Mexico, made available for this study through the courtesy of E. H. Colbert, show that the foot of that genus is essentially similar to that of *Procompsognathus* except that the lateral metatarsals are equal in length. *Coelophysis* thus closely approximates in structure the reconstructed skeleton of *Grallator sulcatus*. While no positive correlation can be made, the Level A footprints attest the presence of a *Coelophysis*-like coelurosaur in the Newark basin of deposition.

## Form-Family GRALLATORIDAE Lull, 1904

## Genus ANCHISAURIPUS Lull, 1904

Type species *A. sillimani* (E. Hitchcock), 1843.

## ANCHISAURIPUS MILFORDENSIS (Bock)

## Figure 3 A

*Gigandipus* ? (*Anchisauripus*) *milfordensis* Bock, 1952, p. 403; pl. 43, fig. 3 (in legend, for "No. 15210" read S488).

*Type*. LC S488, a left pes imprint slightly distorted by the paratype pes of *Chirotherium parvum*.

*Hypodigm*. The type and two other imprints on the same slab; MCZ 135 and 229; AMNH 1981 and 1984. These seven imprints collected by John Eyerman, 1885-1887.

*Horizon*. Upper Triassic (Middle Keuper), Newark series, upper Brunswick formation about 5100 meters above the Triassic base. Level B.

*Locality*. Smith Clark quarry near Milford, Hunterdon County, New Jersey, 1.25 km. north of Delaware River bridge.

*Tentatively assigned*. Certain tracks from the Gettysburg shale (a Brunswick equivalent) near Goldsboro, York County, Pennsylvania (Wanner, 1889, pls. 6, 7, 10). This material was accessioned by the U. S. National Museum in 1888 but is now lost, so that precise comparisons are impossible.

*Diagnosis*. A small, short-footed, broad-based species. The base of claw II lies opposite the crease between the first and second phalangeal pads of digit III, and the tip of claw IV opposite the distal part of the second pad. Metatarso-phalangeal pads II and IV circular and strongly domed, IV nearly twice the size of II. Claws habitually flexed, hastate in outline with basal recesses.

*Morphology*. Collation of the new hypodigm permits some amplification and emendation of Bock's description. Removal of some of the obscuring underclay reveals that the structure which Bock interpreted as a semi-rotated hallux is actually a filled shrinkage-crack which runs from the margin of the slab through metatarso-phalangeal pad II of the type, narrows abruptly, and passes under the label and into the manus of *Chirotherium parvum*. Nowhere is there evidence of a hallux imprint, even

in MCZ 135 where the first phalangeal pad of digit II impressed to a depth of 11 mm. This fact and the osteological differences listed in Table 2 preclude assignment of the species to *Gigandipus*.

Individual variation is apparent in even this small sample. MCZ 135 in particular differs from the others in its relatively shorter digit IV, its large size (103 mm. long vs. 93 mm. in

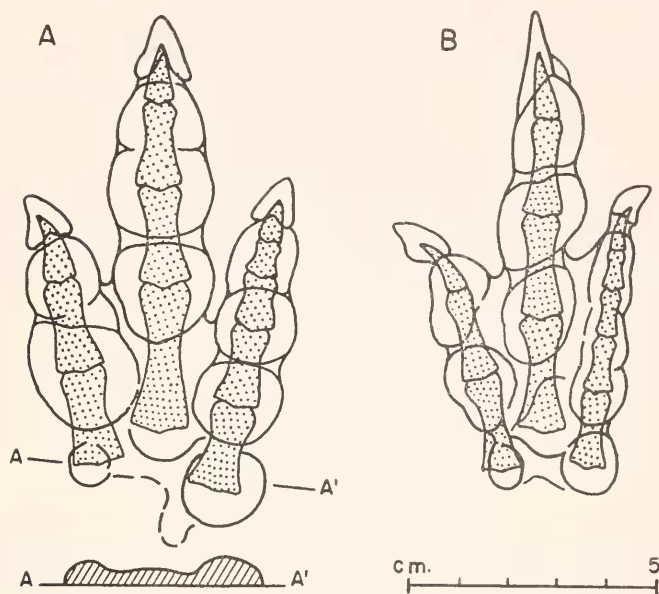


Fig. 3. **A.** *Anchisauripus milfordensis* (Bock),  $\times 3/4$ . Composite outline based on all seven Milford specimens, drawn the size of S488 or MCZ 229. Section A-A' shows the domed lateral metatarso-phalangeal pads. **B.** *Anchisauripus parallelus* (Hitchcock), AMNH 1789,  $\times 3/4$ .

the smallest individual, the type), and its angles of digit divariation (II-13°-III-10°-IV vs. II-15°-III-9°-IV in the type).

The outstanding features of the species—the broad-based foot, the broad, rounded phalangeal pads, and the flexed, hastate claws—have been adequately discussed by Bock. Metatarso-phalangeal pad III is ill-defined, but the dome-like lateral pads are impressed to approximately equal depths with reference to

the rest of the foot. The lack of creases between the phalangeal pads suggests the thick, relatively inflexible plantar padding of a foot which is so specialized for cursorial habits that it retains very little power of grasping. Fringe scales on the median side of digit III are represented by parallel striae, somewhat irregularly spaced, which average 10 to the centimeter. They tell little about the squamation but at least prove that the full width of the digit is recorded.

*Osteology.* A close comparison of Figures 1 and 3 A reveals significant differences in the restored skeletal structure. The individual phalanges of *Anchisauripus milfordensis* are relatively shorter than those of *Grallator sulcatus*, and the unguals may have been, like the claws, shorter and blunter. More important is the difference in the relative positions of the digits. While in *G. sulcatus* the joint of ungual IV lies opposite the joint between phalanges 1 and 2 of digit III, in *A. milfordensis* it lies opposite the waist of phalanx III-2, and the joint between phalanges 1 and 2 of digit III is aligned with the waist of phalanx IV-3. Clearly the central digit of *A. milfordensis* is less advanced with respect to the lateral digits. Additional osteological criteria for comparing this species to other dinosaur footprints will be discussed in a subsequent section.

#### ANCHISAURIPUS PARALLELUS (E. Hitchcock)

##### Figure 3 B

*Material.* AMNH 1789, a sharp impression of a right pes associated with a footprint of *Apatopus lineatus*. Collected by John Eyerman, evidently in the Smith Clark quarry.

*Discussion.* In its form and proportions, especially in the slenderness and lack of divergence of digit IV and the relative positions of the articular pads, this specimen is indistinguishable from footprints of *A. parallelus* found in the Portland formation of Massachusetts and Connecticut. Its reconstructed skeleton corresponds exactly to that of the type specimen as figured by Lull (1953, fig. 42). The Milford footprint, however, is only 6/11 the size of the Massachusetts type. This striking difference in size is associated with no significant difference in proportions: one specimen is a miniature of the other. Despite



our ignorance of trackway characters and range of variation in the Milford form, its form-specific identity is assured.

This is the only footprint species common to the Milford and Connecticut Valley faunules. Whether it represents the same reptilian genus in both areas is of course unknown.

Although no hallux impression is present on the slab, hallux function within populations (or even individual trackways) of *Anchisauripus* is too variable to be of significance in an isolated footprint. Deep creases separate the pads of digits II and III and mark the bases of the strongly flexed lateral claws. Evidently the foot of this dinosaur was rather flexible — perhaps prehensile — at least more so than those of *A. milfordensis* and *Grallator sulcatus*. The fourth digit of *A. parallelus* is longer but clearly less robust than the second, and (at least in the Milford form) appears to be closely joined to the strong third digit. In this respect *A. parallelus* differs from *A. milfordensis*, in which the lateral digits are about equal in robustness and in independence of the third, and differs even more from *G. sulcatus*, in which the second and third digits are joined and the fourth exceptionally independent. The adaptive significance and evolution of these structural patterns can, unfortunately, only be surmised until stratigraphic sequences have been established and skeletal material is available.

## GENUS INCERTUM

### Figure 4 D

A fourth and most peculiar form of dinosaur is represented by a single small, deep imprint of a left pes, MCZ 214. This footprint might be dismissed as an anomaly of impression if a similar specimen had not been found by Wanner (1889) in the Gettysburg shale of York County, Pennsylvania. Wanner's drawing is reproduced as Figure 4 E; the loss of his original at the U. S. National Museum precludes further comparison.

This animal had a broad, compact foot with the central digit projecting only a toe-width beyond the lateral ones. The imprint is deepest on the lateral side (where it is obscured by worm burrows) and in the free lengths of the second and third digits; the rest of the broad "sole" is two to three millimeters shallower. Little rotational or lateral slippage seems to have

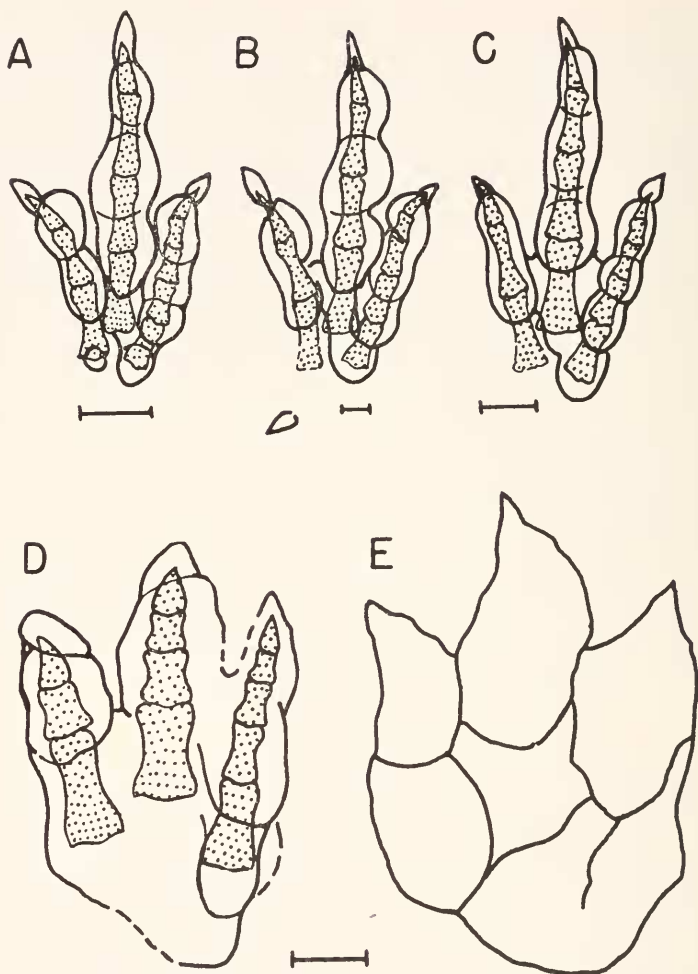


Fig. 4. **A-C**, three dinosaur footprints drawn to common size and orientation, with phalanges restored. **A**. So-called *Grallator gracilis* C. H. Hitchcock, Dartmouth 5023. **B**. Type of *Anchisauripus hitchcocki* Lull, Amherst 56/1. **C**. Plesiotype of *Grallator tenuis* E. Hitchcock, Amherst 17/4. **B** and **C** from Lull. One centimeter scale.

**D**. Tentative reconstruction of genus incertum from Milford, MCZ 214, x 1. **E**. Similar footprint from Goldsboro, Pennsylvania, x 1 (from Wanner). Apparent sharpness of claw tips may be caused by shrinkage cracks.

occurred: the peculiar proportions of the foot are real. But the material available is insufficient for proper analysis and certainly inadequate for taxonomic treatment.

## TAXONOMY OF THEROPOD FOOTPRINTS

Up to this point we have assigned dinosaur footprints from the Delaware Valley to genera best represented in the Connecticut Valley, employing a necessarily typological classification based on similarities and differences in footprint form. This is the traditional approach pioneered by Edward Hitchcock in his "Ornithichnology" of 1836. In Hitchcock's subsequent papers an increasing number of form-taxa were variously grouped and regrouped, with unfortunate wholesale renaming of many units. In this century Lull has achieved a logical taxonomic and nomenclatural reorganization of the Connecticut Valley footprints, a classification which is crystallized in his recent revision (1953).

The three determinable species of theropod footprints from Milford are here assigned to two New England genera which Lull has made the types of two families. Lull's family diagnoses are not, however, mutually exclusive:

**GRALLATORIDAE**: typically small, footprint tridactyl, limbs very long; with or without tail trace.

**ANCHISAURIPODIDAE**: bipedal, tetradactyl; hallux when impressed rotated to the rear; well marked phalangeal pads; anterior claws acuminate but not strongly raptorial; no caudal impression.

In current practice *Grallator* is distinguished from *Anchisauripus* "by greater relative length of stride, smallness of track, and the absence of a hallux impression" (Lull, 1953, p. 153). Within each genus the smaller species are distinguished by size, relative length of digits and of stride, and divarication of the lateral digits. But intermediate forms are common, and isolated or incomplete footprints may be difficult to assign to genus and species even when they are clearly impressed.

Let us examine a specific example of close resemblance. A trackway identified by C. H. Hitchcock as his *Grallator gracilis* (Dartmouth 5023) and the type specimen of *Anchisauripus hitchcocki* Lull (Amherst 56/1) are morphologically so similar

that the differences between them fall within the range of individual variation. Lull's plesiotype of *Grallator tenuis* E. Hitchcock (Amherst 17/4) differs from them chiefly in having digit III slightly farther in advance of the lateral toes (see Figure 4 A-C). All are from the Portland formation of the Turners Falls area, Massachusetts. Their differences in size, gait, and incidence of hallux impression are tabulated below. (Data on the Amherst specimens from Lull.)

	<i>"G. gracilis"</i> Dartmouth 5023	<i>A. hitchcocki</i> Amherst 56/1	<i>G. tenuis</i> Amherst 17/4
Pes length, mm.	51	119	73
Pace length	299	360 to 500	195
Pes: pace length	1:5.9	av. 1:3.6	1:2.7
			(1:3.3 in type)
Hallux imprint	absent (?)	present	absent

What do these differences mean? Size difference may be genetic or ontogenetic. Biometric analyses of true populations of Connecticut Valley footprints have not yet been made, but useful series of measurements from footprints of varied ages and sources have been compiled by Lull (1953). In general, dimensions in each species tend to cluster about a mean, with "occasional gradational footprints which bridge the dimensional gaps between the species." This has been interpreted as evidence of several species of reptiles; but as Lull observes, differences caused by sexual dimetry or by selective representation of age groups (perhaps caused by seasonal migration) are difficult if not impossible to evaluate.

The presence or absence of a hallux imprint appears to be a valid distinction in the huge, broad-soled dinosaur tracks of the Connecticut Valley: in *Eubrontes* the hallux is almost never in evidence, while in *Gigandipus* it usually impresses its entire length. In the *Grallator-Anchisauripus* group, however, the distinction is less clear. Rarely does more than the tip of the hallux claw impress, and even this may be totally absent, as in a four-imprint trackway of *A. sillimani* from Turners Falls (MCZ 252, ex Dartmouth 14, cited in Grier, 1927). In current taxonomic practice the absence of a hallux impression does not debar a specimen from *Anchisauripus* but the presence of one debars it from *Grallator*.

This distinction is unconvincing, especially when we consider that the hallux imprint is typically absent in the smaller and present in the larger members of a morphologically homogeneous series. The foot of a large individual bears relatively more weight than that of a small one, as body bulk is proportional to the cube of the linear dimensions: in walking this greater weight on the metatarsus might well cause the pendant hallux claw to impress more frequently. Similarly, a juvenile dinosaur might be expected to take a relatively longer stride than its more ponderous parent. For these reasons it seems unrealistic to maintain generic, much less familial, distinctions between dinosaur footprint species solely on the basis of such largely extramorphologic characters as size, incidence of hallux imprint, and length of stride.

*I submit that the characters most diagnostic for the classification of footprints as such, as well as most useful for comparison with skeletal remains, are those which reflect the bony structure of the foot.* In most adequately-known varieties of dinosaur footprints the presence of articular swellings and pads permits a reasonably accurate analysis of the skeletal pattern.

To clarify the relationships of the Milford species, therefore, let us compare their restored pedal skeletons with those of other Upper Triassic theropod tracks. For this purpose we must add the phalanges to published figures of the various species, extrapolating to find the length of phalanx III-1 where the position of its proximal end is not indicated by a pad. Because of possible errors in the interpretation of joint position in published figures, this analysis should be considered provisional.

When the skeletons thus reconstructed are compared, the main differences between them are seen to lie in (1) the relative positions of the metatarso-phalangeal joints;<sup>1</sup> (2, 3) the projection of the central digit beyond the lateral ones; and (4) whether digit II or IV projects farther forward. These factors are of course to some extent interrelated. They are more specifically keyed out below, and their distribution among a number of footprint species is shown in Table 2.

<sup>1</sup> This character, the most useful for classification and for skeletal correlations, is also the most difficult to determine in published drawings and faintly-impressed tracks. Close analysis of original material will doubtless necessitate refinements in the subdivision attempted below.

This method of analysis parallels in part the highly instructive comparisons by means of Cartesian diagrams which Lull has appended to his 1953 monograph. (The new insights provided by these diagrams have not, curiously enough, caused Lull to modify his classification of 1915.) My approach, however, concentrates on differences in presumed skeletal structure. By comparing the species of several genera on a single objective basis, rather than matching the previously assigned species of each genus against the type species, it brings out striking inter-generic similarities which might otherwise be overlooked.

### DIAGNOSTIC CHARACTERS

1. A. Metatarso-phalangeal joint III about opposite waist of phalanx II-1 and joint 1-2 of IV.  
B. Metatarso-phalangeal joint III about opposite proximal end of II-1 and waist of IV-1.  
C. Metatarso-phalangeal joint III about opposite that of II and joint 1-2 of IV.
2. A. Joint of ungual II about opposite joint 1-2 of III.  
B. Joint of ungual II about opposite waist of III-2.  
C. Joint of ungual II about opposite joint 2-3 of III.
3. A. Joint 1-2 of III about opposite joint of ungual IV.  
B. Joint 1-2 of III about opposite joint 3-4 of IV.  
C. Joint 1-2 of III about opposite joint 2-3 of IV.
4. A. Digit II projects farther anterior than IV.  
B. Digits II and IV project about equally far.  
C. Digit IV projects farther anterior than II.

Let us now attempt a generic regrouping of these species:

I. GRALLATOR, type species *G. cursorius*. *G. sulcatus* clearly belongs to this group despite its atypical forward-set central digit and subequally projecting lateral digits. *G. tenuis* appears to be intermediate between groups I and II, resembling the latter especially in the relative positions of the metatarso-phalangeal joints. A surprise here is that *Otouphepus minor*, though superficially similar to *O. magnificus*, is otherwise quite unlike it and shows itself to be a *Grallator* in size and morphology. This species, based on a single isolated footprint, is of questionable validity.<sup>2</sup> *G. formosus*, included doubtfully by Lull because of its long stride and lack of a hallux imprint, belongs rather to Group III.

<sup>2</sup> The nature of *Otouphepus* is discussed in Appendix 1.



TABLE 2: COMPARISON OF SOME UPPER TRIASSIC THEROPOD FOOTPRINTS

	1.	2.	3.	4.
Grallator cursorius	A	A-B	B	A
G. euneatus	A	A	B	A
G. gracilis <sup>3</sup>	A	A	B	?
Otouphepus minor	A	A	B	B
G. sulcatus (Figure 1)	A	A	A	B
G. tenuis (Figure 4 C)	B	A-B	B	B
Anchisauripus sillimani	B	B	B	A
"A. exsertus" plesiotype, Amherst 54/1	B	B	B	A
A. hitchcocki (Figure 4 B)	B	A-B	B	B
Dartmouth 5023 (Figure 4 A)	B	A-B	B	B
Anchisauripus tuberosus	B	A-B	C	C
A. exsertus	B	B	C	C
A. parallelus (Figure 3 B)	B	B	C	C
A. australis (Argentina)	B	B	C	C
Jeholosauripus ssatoi (Manchuria)	B	B	C	B-C
Grallator formosus	B	A-B	C	C
Otouphepus magnificus	?B	B	B-C	B
A. minusculus	B	A-B	C	B
A. milfordensis (Figure 3 A)	B	A	B-C	B
Eubrontes giganteus	B	B	C	B
Gigandipus caudatus	C	C	B	A

II. ANCHISAURIPUS (sensu stricto). *A. sillimani*, the type species, shows closest affinities with *A. hitchcocki*, *G. tenuis*, and the Dartmouth trackway assigned to *G. gracilis*. Amherst specimen 54/1, figured by Lull (1904, fig. 7; 1915, fig. 41; 1953, pl. 10, fig. 11 — but not fig. 41 which is mis-captioned Amherst 54/1 but actually shows 16/6, the type) as *Anchisauripus exsertus* proves instead to be a large *A. sillimani*. (The same is true of Amherst 34/14 in Lull's pl. 10, fig. 12.) Much original material of these forms must be compared before taxonomic decisions can be reached.

<sup>3</sup> Lull's figure of the *G. gracilis* plesiotype appears rather different from C. H. Hitchcock's original figure of the type (in E. Hitchcock, 1865, pl. 9, fig. 7). Perhaps the latter figure is inaccurate or the plesiotype is misassigned.

III. *ANCHISAURIPUS* (sensu lato). Quite a distinct aspect is shown by the larger species of *Anchisauripus* (earlier assigned to *Brontozoum*), in which digit IV is set well forward. Within this group *A. tuberosus*, *A. exsertus* and *A. parallelus* are so similar that they might be considered a single variable species. *A. australis* Lull (1942) from the Pagazano beds of Argentina is a typical representative of the group. *Jeholosauripus ssatoi* from the "Eo-Mesozoic" of Manchuria (Shikama, 1942) clearly belongs here, as do *Grallator formosus* and *Otouphepus magnificus*. Suppression of the latter genus and species (Baird, 1956; see Appendix I) will remove them from consideration. *A. minusculus* is, as Lull notes, a sharply defined species; it seems to be intermediate between the other members of this group and *Eubrontes giganteus*. *A. milfordensis* is also somewhat transitional but is referred to Group III because of its forward-set central digit and its small size.

Strict consistency would require that Group III be distinguished as a separate genus of the Grallatoridae. Unfortunately there is no Hitchcockian name available for these forms,<sup>4</sup> and rather than make major nomenclatural changes on the basis of this preliminary survey, I will for the present follow Lull's terminology.

The dinosaurian footprint associated with *Chirotherium lulli* at Milford (Baird, 1954, fig. 2 C) and the specimen from York County, Pennsylvania, which Hiekok and Willard (1933, fig. 6 B) assigned to *Anchisauripus sillimani* are so different from the forms in Table 2 (and from the Anomoepodidae as well) in the position of their lateral digits that they cannot be classified in the key used here. They apparently belong to a distinct family, which is represented in Europe by *Coelurosaurchnus* (sensu stricto: see Baird, 1954, p. 182). This family is apparently not represented in the Meriden and Portland formations of the Connecticut Valley.

<sup>4</sup> The appropriate and previously used name *Brontozoum* is excluded by nomenclatural technicalities which are discussed in Appendix II.

## Order THECODONTIA

## Suborder PSEUDOSUCHIA

## Form-family CHIROTHERIIDAE Abel, 1935

## Genus CHIROTHERIUM Kaup, 1835

## BRACHYCHIROTHERIAN GROUP

*Diagnosis.* Specialized Upper Triassic chirotheriids lacking a thumb-like fifth phalangeal segment distinct from the metatarso-phalangeal pad.

## CHIROTHERIUM PARVUM (C. H. Hitchcock), 1889

Figures 5, 6 A; Plate 1, figure 2.

*Otozoum parvum* C. H. Hitchcock, 1889, pp. 122, 123, 127.

*Otozoum parvum*. Lesley, J. P., 1889, pp. 571-573, 3 figs.

*Otozoum parvum*. Lyman, B. S., 1894, p. 214; 1895, pl. 608, figs. 1-3.

?*Otozoum parvum*. Lull, R. S., 1904, p. 515.

?*Chirotherium parvum*. Lull, R. S., 1915, p. 226, fig. 77.

*Chirotherium* (?) *parvum*. Lull, R. S., 1917, p. 119.

*Chirotherium parvum*. Peabody, F. E., 1948, p. 346.

*Chirotherium parvum*. Bock, W., 1952, pp. 410-414; pl. 41 with plate title 42; pl. 42 with plate title 41; pl. 43, fig. 2 (for Paratype No. S488 read Holotype No. S490).

*Chirotherium copei* Bock, 1952, pp. 414-415; pl. 43, fig. 1 (for x 1 . . . No. S491 read x 1/2 . . . ANS 15210).

*Chirotherium* [*copei*]. Richards, H. G., 1953, fig. 176.

*Chirotherium parvum*, *C. copei*. Baird, D., 1954, pp. 174, 175.

*Type.* LC S490, designated by Bock, a large right manus-pes set; the missing posterior half of metatarso-phalangeal pad V is preserved on MCZ 212.

*Hypodigm.* The type, LC S488 and MCZ 211 probably represent two individuals of similar size. ANS 15210 (type of *C. copei*), MCZ 209, MCZ 210 and AMNH 2257 appear to represent one individual. Horizon, locality and collector as for *Anchisauripus milfordensis* (collector of ANS 15210 is unknown).

*Diagnosis.* Phalanges of pes digit V reduced and included in the metatarso-phalangeal pad; pes digits IV and V clawless; narrow, curved claws on pes digits I to III borne high above the thickly padded plantar surface and divergent laterally; metatarso-phalangeal pads III and IV coalesced.

*History.* The type of this remarkable species has been validly designated by Bock, yet curiously enough this may not be the primary specimen on which Hitchcock's species concept was based. The original description, fragmented between two sections of a notoriously imprecise paper, designated no type and was not illustrated. Outline figures of the species, however, appeared the same year in Lesley's hodgepodge "Dictionary of Fossils" with this notation:

"**Otozoum parvum**, n. sp. C. H. Hitchcock. Fig. 1, hind foot track; fig. 2, fore foot track (both *natural size*); fig. 3, reduction of the two foot prints to show in what relation they stand to each other on the slab of *Trias* sandstone in the quarries at Milford, on the New Jersey side of the Delaware river, about thirty miles above Trenton. Discovered and traced in outline by Prof. C. H. Hitchcock. (See MS. letter, Dec. 1888.) *Upper Trias*.—NOTE. When first seen it was thought to be a *Cheirotherium* track, but it has only four toe marks on each foot." (Lesley, 1889, pp. 571-572.)

These figures, though reprinted by Lyman (*loc. cit.*), have hitherto escaped the attention of bibliographers and researchers alike.

A second outline drawing by Hitchcock, first published in 1915 by Lull, is not identical with the first. Both, however, show the cast of a right manus-pes set, and they are so similar in proportions and particularly in the relative positions of the manus and pes (seldom duplicated exactly in a chirotheriid trackway) that both probably represent the same specimen.

Only one of the existing specimens, the type of *C. copei* Bock, closely resembles these drawings in the features cited. Hitchcock's statement that the pes "is 5 inches long besides 2½ inches of heel" applies to this specimen but cannot refer to the Lafayette College types. Now the early history of the *C. copei* slab, which Bock obtained (misabeled as to locality) from the effects of an amateur collector of fossils, is obscure; yet the internal evidence indicates that this specimen or one remarkably like it constituted the undesignated, conceptual type of Hitchcock's species. Thus *Cheirotherium copei* may be an objective as well as a subjective junior synonym of *C. parvum*.

*Variation.* The three individuals (or so) represented in the population show a good deal of variation and (if the isolated

tracks are correctly assigned) some intra-individual variation as well. These irregularities are, of course, in addition to those caused by differences in impression and preservation. The type and paratype may represent the left and right feet of the same individual. Pes digit I of the type, however, is relatively longer: its claw-mark extends nearly to the tip of digit II instead of to



Fig. 5. *Chirotherium parvum* (C. H. Hitchcock), right manus-pes sets,  $\times 1/3$ . A. Type of *C. copei*, ANS 15210. B. Type of *C. parvum*, S490 + MCZ 212, showing striated digit-tip impressions.

the base of the distal pad on II, as in S488, MCZ 210, and ANS 15210. MCZ 209 is intermediate in the length of digit I but is otherwise nearly a mirror image of ANS 15210. In relative width of the digit I-IV group and in robustness of manus digit I the type and paratype resemble each other and differ from the smaller, slenderer specimens which are referred to the "*C. copei*" individual (cf. Figure 5).

In my opinion these differences are insufficient to distinguish two species. Individual, age, and sexual variation are to be expected in the Milford reptile population. Differences observed within the hypodigm are minor and do not appear to be correlated. All the specimens exhibit a syndrome of specializations which is unique within the form-genus *Chirotherium* and almost certainly represents a single reptilian genus. Sympatric species of this unusual genus are of course possible, but since similarities greatly outweigh differences, the burden of proof would seem to lie with the splitter.

*Morphology.* Most of the salient features of this species have been described by Lull and Bock. Curiously enough the pes claws, which are present in every specimen and constitute one of the most distinctive features of the species, remain undescribed and their existence has only been surmised (Bock, 1952, p. 412). These claws were carried high above the plantar surface so that only their tips ordinarily impressed. Spalling of the natural casts obscures the relationships, but where measurements can be made the base of the claw lies at least 6 mm. above the sole of the digit tip.

Instead of forming a linear extension of the digit these claws are turned strongly outward, so much so that the first and second must have nearly touched the sides of the digits lateral to them. The claws were carried in the normal vertical position; their lateral divergence of some  $35^{\circ}$  seems to be the effect of an oblique ungual articulation, for the digits themselves are otherwise nearly straight.

Claw I is long and narrow and slightly curved laterally; its distal half forms a convex ventral keel rather than a point. Claw II, the heaviest, is carinate along its concave ventral profile but ends in a conical point, sometimes blunted by wear. Claw III is similarly curved and pointed. Of course the depth of the claw-tip impressions has been exaggerated when the toes dug in at



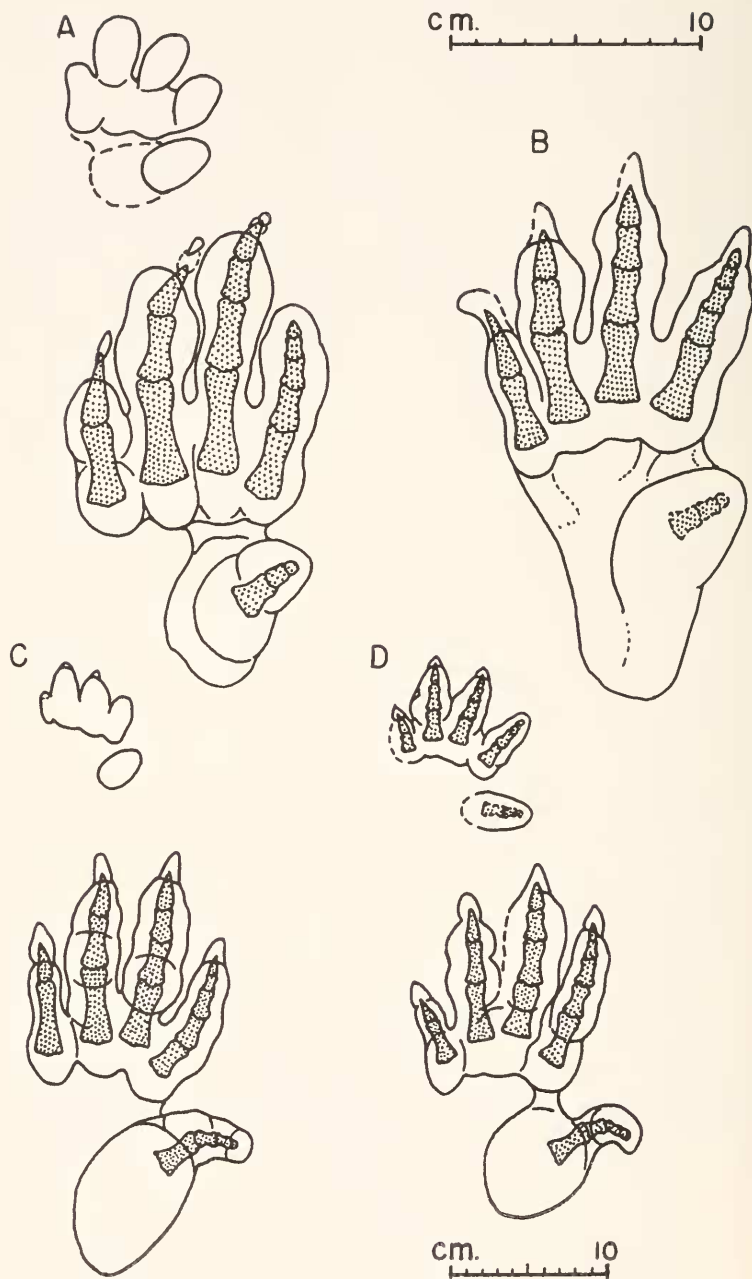
the end of the propulsive phase. Digit IV appears to be clawless in all five specimens, even where the digit-tip impression is 8 mm. deep — an anomalous condition, for a well-developed claw IV characterizes most other chirotheriids.

The vestigial fifth pes digit, so different from the well-developed "thumb" of most chirotheriids, is a striking feature of *Chirotherium parvum*. A single ovoid pad underlies the phalanges and the metatarso-phalangeal joint. As in several other Keuper species (Baird, 1954, p. 174) this pad has migrated somewhat medially from the primitive position, so that the distal end of metatarsal V must have underlain the shaft of IV. Only slight marginal indentations and a suggestion of separate planar thickenings distinguish the phalangeal section of the pad, which is scarcely longer than its width and narrows abruptly to an ogival, clawless tip.

Almost as distinctive as this digital "heel" is the pattern of plantar pads underlying the metatarsal cross-axis. The metatarso-phalangeal pads form a straight line of low bosses across the posterior edge of the sole; a single flat, subcircular pad underlies the bases of digits III and IV. This condition is quite unusual among chirotheriids. A pad common to two digits occurs in both large-manus and small-manus species but this pad is always central, joining the bases of digits II and III, while the pads of I and IV are distinct. Only in *Otozoum* do we find a single pad for digits III and IV.

Unlike the pes, the manus is typically chirotherioid in form and shows little specialization except that claws are apparently absent and digit V is only slightly offset. (Digits IV and V are definitely clawless but evidence on the others is inconclusive.) The fifth digit is not small and abortive, as Bock terms it, but normal in length and robustness. In the exceptionally deep paratype imprint, moreover, its pad is revealed as merely the slenderer distal part of a large ovoid "heel" which extends postero-medially to a point in line with the axis of digit I. (See Bock, 1952, plate 41 with plate title 42.)

The imprint made by this "heel" pad is 13 mm. deep and slightly undercut laterally. Its steep posterior and postero-medial margins are in strong contrast to the gently sloping margins of the pedal "heel" and suggest that the fifth metacarpal



was held nearly vertical as the manus was implanted. The other metatarsals apparently sloped less steeply than the fifth but considerably more steeply than the metatarsal bundle. This evidence of a more digitigrade manus supports the correlation of *Chirotherium parvum* with a reptile of bipedal ancestry in which the forelimbs were shorter than the hind, and in which such a functional lengthening of the forelimb pendulum would have made for more efficient quadrupedal locomotion.

The paratype manus imprint is divided by a large shrinkage crack which, oddly enough, does not exaggerate its width but rather compresses it laterally so that the third and fourth digit impressions are coalesced. The type imprint of *Anchisauripus milfordensis* is also compressed where it is crossed transversely by the same crack. My explanation for this phenomenon is that the shrinkage crack antedated the footprints (see Soergel, 1925, figs. 45-48 for other examples). Before the sand which now forms the natural casts was washed over the recording surface the clay was flooded and consequently expanded, narrowing the shrinkage cracks and thus compressing the footprints. Ich-nologist, take warning: things are not necessarily what they seem.

CHIROTHERIUM EYERMANI Baird, n. sp.

Figure 6 B; Plate 2

Eyerman's chirotherium. Baird, 1954, pp. 174, 175-176.

*Type.* MCZ 134, an isolated left pes imprint collected by John Eyerman in 1887; the only known specimen. Horizon and locality as for *Anchisauripus milfordensis*.

*Diagnosis.* A moderately large species with slender digit I, short, robust pes digits II-IV bearing heavy claws at sole level, and greatly shortened, hoof-like digit V enclosed in a single pad. Digit IV shorter than II. Metatarsal cross-axis oblique; plantar padding undifferentiated. Manus and trackway unknown.

Fig. 6. Brachychirotherian (A, B), small-manus (C), and large-manus (D) chirotheriids with attempted skeletal restorations. A. *C. parvum*, composite of entire hypodigm. B. *C. eyermani* n. sp., type (MCZ 134). C. *C. lomasi*, Keuper of Storeton, Cheshire (Yale Peabody Museum 3762, a small individual). D. *C. barthii*, Moenkopi of Cameron, Arizona (University of California Museum of Paleontology 37315). A-C x 1/3, D x 1/5.

*Morphology.* The single footprint of this species, which is impressed to a maximum depth of 40 mm. below ground level, illustrates a fact often overlooked: a footprint is not a cast of the underside of a foot but a composite record of the foot in motion. The effects of structure, function, and preservation are combined in the specimen and must be separated by analysis. If we eliminate the functional distortions of the imprint (which are revealed by slippage marks and variously inclined groups of striations produced by the claws and scales) the foot itself appears to have the form shown in Figure 6 B.

A tendency toward functional tridactyly is evidenced by a strengthening of the three central digits at the expense of the first and fifth. Indeed, the soft mud was resistant enough to bend the feeble first digit upward at a  $20^\circ$  angle to the second. The inward-turned imprint of claw I may be atypical, for such a deflection occurs sporadically in chirotheriid trackways. The undulant outlines and almost undifferentiated pads of digits II-IV are reminiscent of *C. parvum*, but in strong contrast are the straight, massive claws with their slightly convex soles forming an unbroken continuation of the general plantar surface. Also distinctive is the shorter, more divaricate digit I-IV group with its more oblique metatarsal cross-axis and flat, subrectangular sole. From the bases of digits I and IV a pair of ridges which appear to represent the *flexores digitorum breves* extend proximally, converging toward the tarsus. The slope of the longitudinal arch, a feature rarely revealed in chirotheriid footprints, indicates that the first four metatarsals formed an angle of  $155^\circ$  with the proximal phalanges as the pes was implanted.

Digit V, revealed in unusual detail in this footprint, closely resembles that of *C. parvum* except that its phalangeal segment is less pointed and is quite undifferentiated from the metatarsophalangeal pad. This "heel" pad is relatively flat instead of ovoid as in *C. parvum*; it is impressed about 9 mm. deeper than the ventral surface of the longitudinal arch. A definite bridge connecting the "heel" to the base of digit IV suggests a ligamentous connection between the distal ends of the metatarsals. From the sole at the tip of digit V a small falciform web curves upward and joins the side of digit IV, well above its sole.

The distal margin of digit V shows a striation of flutings which average 2.5 mm. between crests. This fluting resembles the striated impressions of claws III and IV and is quite distinct from the scalloped profile produced by fringe scales 3 mm. wide on the medial border of digit II. The greatly reduced fifth digit thus appears to have been tipped with a broad nail or hoof. Such a structure has been reported in no other species of *Chirotherium*.

### Osteology of Level B Chirotheriids

The thick, little-differentiated plantar padding in *Chirotherium parvum* and *C. eyermani* makes it impossible to locate all the joints and thus to determine precisely the phalangeal formula. Representative phalangeal patterns may, however, be deduced in other species where articular swellings are well developed. Figure 6 D shows the arrangement in *C. barthii*, the common large-manus species of the European and American Lower (or Middle) Triassic. Here the formula indicated is manus 2-3-4-?4-?3, pes 2-3-4-5-?4. An Upper Triassic member of the same group, *C. lulli*, is basically similar but appears to have only three phalanges in the thumb-like fifth digit (Baird, 1954, fig. 2 A). In the best-known small-manus species, *C. lomasi* of the English Keuper (Figure 6 C), a formula of 2-3-4-5-?4 is evident in the pes but no skeletal pattern is discernible in the hoof-like manus.

In preparing the skeletal restorations of *C. parvum* and *C. eyermani* I have indicated joints at localized thickenings in the sole wherever possible, and have extrapolated as little as possible from the structure of other species. In *C. parvum* a slight differentiation in the coalesced pad of pes digit V suggests the presence of three phalanges, so by analogy the same number is hypothesized for *C. eyermani*.

### Classification of Chirotheriids

Peabody, working chiefly with Lower Triassic species, has separated the better-known chirotheriids into a typical or large-manus group and a specialized small-manus group. Ratios of manus to pes area in representative members of each group are

tabulated below, in order of decreasing relative manus size. (Areas include only the digits and metapodio-phalangeal pads. These ratios, based on single manus-pes sets, are not necessarily typical of the species listed.)

Large-Manus		Small-Manus	
<i>C. lulli</i> Bock	1:2	<i>C. coltoni</i> Peabody	1:5.7
<i>C. storetonense</i> Morton		<i>C. marshalli</i> Peabody	1:5.7
	ca. 1:3	<i>C. lomasi</i> Baird	1:6.6
<i>C. minus</i> Sickler	1:3		
<i>C. wondrai</i> Heller	1:3.4		
<i>C. barthii</i> Kaup	1:3.6		

In *Chirotherium parvum* the type manus is too incomplete for areal measurement but ANS 15210 furnishes reliable figures of 25 cm.<sup>2</sup> for the manus and 112 cm.<sup>2</sup> for the pes. (Bock's measurement of 85 cm.<sup>2</sup> for the pes apparently omits the "thumb" pad.) The resulting manus-pes ratio of 1:4.6 falls between the ranges of the two groups. Except for the closeness of digit V to its fellows the manus of *C. parvum* is more similar to that of the large-manus species than to the compact, hoof-like forefoot of the small-manus group. Unfortunately, nothing is known of the manus in *C. eyermani*.

The shortening of pes digit IV, moderate in *C. eyermani* but extreme in *C. parvum*, would seem on typological grounds to ally these species with the small-manus group, in which such a shortening is characteristic. In terms of function, however, this condition is obviously essential to the maintenance of symmetry in any walking foot in which the fifth digit has undergone reduction. Other examples are found in the feet of dinosaurs, crocodiles and birds (where apparent exceptions such as *Gavia*, *Pelecanus* and *Hesperornis* prove the rule, since walking is not the primary function of the foot). Thus the shortened fourth digit in the Milford species is functionally correlated with the vestigial fifth digit and indicates parallelism rather than affinity with the small-manus group.

The Level B chirotheriids thus appear to represent a lineage distinct from the small-manus group although paralleling it in adaptive modifications and similarly derived from a primitive large-manus stock. This lineage has been progressively modified



to a point where it must be considered a distinct sub-generic group, characterized by the short, oval, heel-like fifth pes digit.

This group, here recognized in North America for the first time, is represented by specimens from several horizons in the Middle Keuper of Germany (Heller, 1952). The oldest of these, an imperfect pes imprint from the Blasensandstein of Franken, was described by O. Kuhn (1936) as *Chirotherium* sp. In size and proportions it shows a decided resemblance to the Level B species, particularly *C. eyermani*, differing chiefly in the greater length of digit V.

A rather similar but slightly younger form is *Chirotherium thuringiacum* Rühle von Lilienstern (1938) from the Platten-sandstein (km 4 zeta) of Thüringen. This species recalls *C. eyermani* in its short, divergent pes digit I-IV group. It resembles *C. parvum* in its round, apparently clawless digit tips; and the manus with its plump, clawless toes and close-set, medially shifted digit V is strikingly similar.

Slightly higher in the Middle Keuper, in the Semionoten-Sandstein of Franken, occurs a group of chirotherioid footprints which Beurlen (1950) has named *Brachychirotherium hassfurtense*. Though the specimens figured are somewhat heterogeneous they all show a foot structure like that described above, with apparently clawless digits and an abbreviated "thumb." The latter appears so inconsistent in its size, position, and orientation, and the relative lengths of the other digits are so variable from specimen to specimen, that definitive diagnosis of the species (singular or plural) is impossible. Unfortunately, all these German forms have been described from individual footprints rather than analyzed on the basis of a composite of each population. Specific distinctions are by no means clear, particularly as no types have been designated, and the differences carefully tabulated by Heller may or may not be significant. Nevertheless these Middle Keuper species from Germany are clearly referable to the same group as *C. parvum* and *C. eyermani*.

For this group Beurlen has established the separate genus *Brachychirotherium*. Since the differences between this and the large-manus group are little greater than those which distinguish the small-manus group from both, I prefer to broaden slightly the scope of the form-genus *Chirotherium* to include a third

sub-generic group for which Beurlen's name may appropriately be retained. Following the example of Peabody I assign this group no formal Linnaean status.

### Evolutionary Tendencies

The modifications seen in this brachychirotherian group are clearly consistent with the general evolutionary trend of Keuper chirotheriids which I have previously outlined (1954, p. 188): the tendency of an osteologically pentadactyl stock to become functionally tetradactyl through elimination of the lateral proping function of the fifth pes digit. In the brachychirotherian group this was being accomplished by several means: by shifting the distal end of the unshortened metatarsal V more or less medially, beneath and behind the shaft of metatarsal IV; by progressively shortening and straightening the fifth digit to minimize its lateral projection; and ultimately by incorporating the metatarsal and phalanges into a single, inflexible heel structure. During this process a gradual shortening of digit IV tended to maintain the symmetry of the foot. Concomitantly the manus became smaller and more compact.

Although — most unfortunately — we have no trackways from which to determine the locomotor habits of the group, it seems inescapable that these modifications promoted more efficient locomotion, presumably cursorial and (as Rühle von Lilienstern points out) showing bipedal tendencies in some members. Increasing competition from the expanding and diversifying stocks of saurischian dinosaurs may well have channeled chirotherian evolution along these lines.

Changes in foot structure and locomotor pattern are of course only a part of the overall adaptive modification which must have taken place in the brachychirotherian group. Only a part, yes: but surely an important one, for, as I have shown (1954, p. 174), convergent modifications were independently taking place in Keuper representatives of both the large-manus and small-manus groups. Apparently the chirotheriid locomotor equipment of early Triassic time had been found inadequate for the conditions of mid-Keuper life.

The chirotheriid response to changing conditions was, however, insufficient. We have noted that even in the most special-

ized species, *C. parvum* and *C. eyermani*, the once thumb-like fifth digit was still functional in modified form. Dinosaurs and small pseudosuchian or proto-crocodylian types such as *Batrachopus*, in which locomotion had become more efficient through the loss or atrophy of the fifth digit, eventually replaced *Chirotherium*. Huge size and bipedality (along with other specializations yet unknown) permitted a lone descendant of the chirotheriid stock, *Otozoum*, to survive until the close of Newark time — but that is another story.

### Osteological Correlations

That chirotheriid trackways are the products of various pseudosuchian reptiles is now generally accepted. Beyond this premise the foregoing discussion has avoided assumptions as to the identity of the Milford trackmakers, attempting instead an objective analysis of the ichnological evidence as such. The possible position of these trackmakers among the Pseudosuchia can now be examined.

At present the pedal skeletons of most Upper Triassic pseudosuchians are too inadequately known to permit useful comparisons with the three Milford species of *Chirotherium*. The relatively conservative large-manus species *C. lulli* has been interpreted as a small, persistently quadrupedal ornithosuchid not too different from the presumably ancestral form *Euparkeria*; but closer comparisons are impossible. Among middle to late Triassic reptiles which might be compared to the brachychirotherian species only two, *Prestosuchus* and *Typothorax*, are represented by even relatively complete foot material.

As restored by Peabody (1948, fig. 39 B-C<sup>5</sup>) the pes of *Prestosuchus* is broad and short-toed, suggesting (as Peabody notes) the brachychirotherian *C. thuringiacum* Rühle. Lack of the tip of digit IV and all phalanges of digit V, however, precludes for the present any correlation of *Prestosuchus* with one or another of the chirotheriids. Certainly the phalanges are relatively much shorter than those restored for the Milford footprints. As Huene (1944) records only a single phalanx from the manus, Pea-

<sup>5</sup> Peabody has followed Huene in reversing the proximal overlap of the metatarsals although the natural relationship is preserved in the specimen itself — cf. Huene, 1944, pl. 20, fig. 4 a-b.

body's very plausible reconstruction of the manus digits cannot be used for comparison.

Despite the strong contrast in habitus between the relatively narrow-bodied, lightly-armored, predaceous *Prestosuchus* and the broad-backed, heavily-armored, necrophagous *Typothorax* (Sawin 1947), the two are strikingly similar in phalangeal pattern. Thus the general aspect of *Typothorax* is brachychirotherian-like but its short phalanges seem to eliminate it from comparison with the Milford footprints. The manus is decidedly chirotherian in form although its fifth digit appears to have been somewhat weaker than that of most chirotheriids. Areas of the digit I-IV groups in manus and pes bear a ratio of about 1 to 3, a ratio found in *C. thuringiacum* and some large-manus chirotheriids. If brachychirotherian trackways were available the pedal similarities between *Prestosuchus* and *Typothorax* should cause little difficulty in correlation, for the swift-striding predator must have left a much narrower trackway than its broad-beamed, ponderous relative. But pending the discovery of such additional evidence the systematic positions of the Level B pseudosuchians must remain uncertain.

## Order THECODONTIA

### Suborder PHYTOSAURIA

#### Form-family APATOPODIDAE Baird, nov.

#### Genus APATOPUS Baird, nov.

Type species *A. lineatus* (Bock), 1952; family and genus monotypic.

*Diagnosis.* Quadrupedal trackway with pace angulation about  $108^\circ$ , pes but not manus toed-out. Feet pentadactyl with well-developed articular swellings and sharp claws; manus short and symmetrically radiate, pes long and narrow with digits in order of increasing length V-I-II-III-IV.

#### APATOPUS LINEATUS (Bock)

#### Figures 7, 8; Plates 3, 4

*Otozoum* (?) *lineatus* Bock, 1952, pp. 408-409, pls. 48, fig. 1 and 46, fig. 1 (mistitled "Type No. 15230" for LC S489). Probable earlier syn-

onymy in Table 1; the variety of past assignments suggested the generic name. Diagnostic characters are those of the genus.

*Type.* LC S490, a left manus-pes set (Bock's type) plus MCZ 212, the succeeding right set of the same trackway.

*Hypodigm.* The type, S489, and MCZ 213, presumably three adults; AMNH 1789 and 2258, smaller individuals; AMNH 2259 and MCZ 214, juvenile (same individual?). Source data as for *Anchisauripus milfordensis*.

*Trackway.* By a remarkable and fortunate coincidence a tiny contact area between corners of the Lafayette and Harvard slabs permits the reconstruction of the type trackway. (This contact crosses the "thumb" of the *Chirotherium parvum* type, cf. Figure 5 B.) Trackway parameters determined by direct measurement or by extrapolation (\*) are tabulated below. In the first three the reference point is the center of metatarso-phalangeal pad III:

Pace, angular	42.5 cm.
Stride	*70 cm.
Pace angulation	*108°
Gleno-acetabular length (approximate)	*52 cm.
Interpes width (between median margins)	13.7 cm.

*Pedal morphology.* The additional material now available permits analysis which was impossible with the incomplete, obscure, single manus-pes set on which the species was based. A composite restoration derived from all this material is presented in Figure 7. The digits of both manus and pes are shod with domed, oval articular pads separated by slender waists, so that joint positions are apparent in profile as well as in section. The claws are slender and rather crocodilian in the manus but appear heavier and more triangular in the pes, where rotation during withdrawal has obscured their exact form. As the plates show, laterally flexible ungual articulations permitted much lateral movement in both manus and pes claws.

The manus is nearly symmetrical around digit III, the metacarpo-phalangeal pads forming a regular semicircle, so that in form and proportions it recalls the manus of *Mesosaurus*—an aquatic form. A phalangeal formula of 2-3-4-?5-?3 is indicated. In normal function the manus was digitigrade and only in the deepest imprint did the palm register (Plate 4, figure 1).

The pes with its long fourth digit and peculiar sole is quite

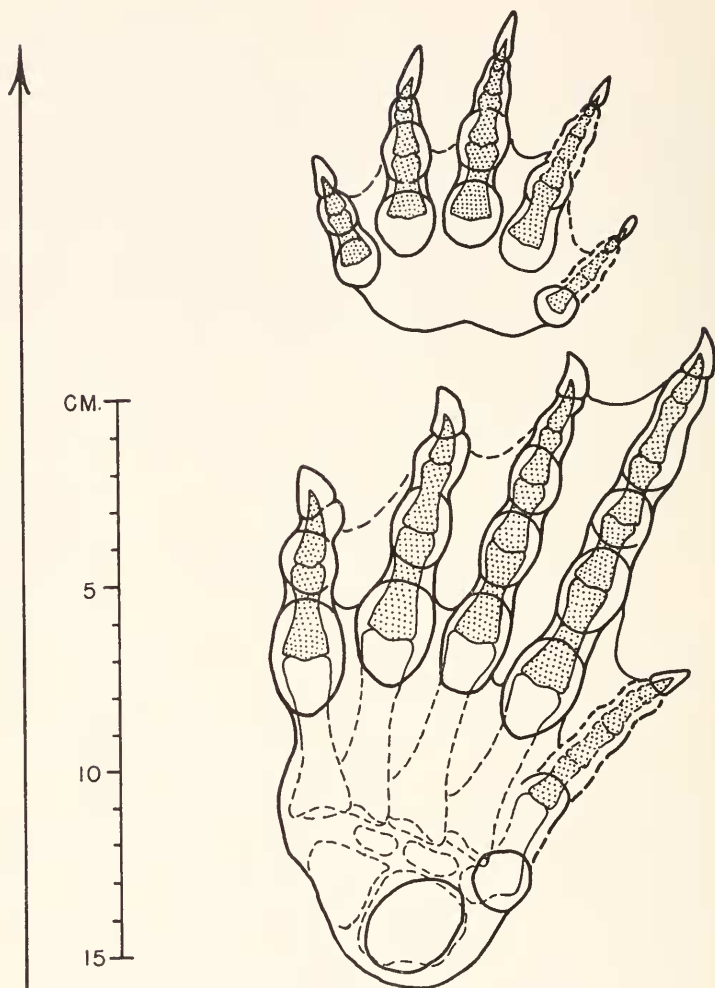


Fig. 7. *Apatopus lineatus* (Bock), composite restoration based on type (S490 + MCZ 212) with parts of digits IV and V restored from other specimens,  $\times 1/2$ . Arrow represents midline of trackway.



distinct from other Triassic footprint types. At first glance it appears to show affinities with primitive reptilian pedes of the pelycosaur or captorhinomorph type, but the fact that metatarsal IV is slightly shorter than III (rather than the reverse) indicates that digit IV has been secondarily lengthened by hypertrophy of its phalanges. A similar secondary lengthening of the phalanges of digit IV occurs in the manus of the marine turtle *Chelonia mydas* (cf. Abel, 1912, fig. 111). Aquatic adaptation is the most obvious explanation for such a modification, and this interpretation is supported by the evidence of interdigital webs. Although the length and position of the short fifth digit are evident its structural details are obscure; my conjectural restoration shows four phalanges, making the pes formula 2-3-4-5-?4.

The extent of interdigital webbing in *Apatopus* is uncertain, particularly because the pes in walking was often laterally compressed so that web margins would have left no mark. The best-represented web connects the bases of pes claws III and IV, an arrangement quite in contrast to that in living crocodilians, in which the deeply recessed webs occupy only part of the interdigital area. Additional (though circumstantial) evidence for the presence of webbing is the fact that digits IV and V are adequately recorded only in the deepest footprint, which suggests that distribution of the animal's weight over a webbed area effectively reduced the depth of impression. Here as in other fossil footprints, unfortunately, the evidence is less than satisfactory.

Traces of the squamation are preserved only in the juvenile MCZ 214 (Plate 4, figure 1). Here the digits of manus and pes show a fine beaded or pustulose texture which compares closely with the skin of corresponding areas in a juvenile *Gavialis gangeticus*.

Except in the deepest impressions the sole is very indistinctly recorded. Some understanding of it can nevertheless be obtained by collating outlines printed from latex molds of several specimens. On the medial margin a bulge marks the position of the first metatarsal's proximal head, and opposite this is a circular pad which must have underlain the fifth metatarsal. On this basis the first four metatarsals have been restored in normal alignment. Its distinct individual pad suggests that the proximal end of metatarsal V was less elevated than that of metatarsal IV;

if so, then the fifth metatarsal probably articulated with the tarsus by a hooked, dorso-medially directed process. Postero-medial to this area a large, subcircular calcaneal pad forms the heel of the footprint. The possible presence of a tuber calcanei is suggested by the relatively deep impression of this pad. Though plausible, this interpretation of the tarso-metatarsal area rests on admittedly tenuous evidence.

*Variation.* Aside from striking variations in the manner of impression, which are apparent in the plates, the *Apatopus* footprints reveal only minor differences among the six (or so) individuals of the population. Chief of these is size: the smallest individual, AMNH 2259, has a pes length just half that of the type (as restored). Osteological analysis reveals the structural unity of these footprints which might otherwise be assigned to a number of form-species.

#### Affinities of *Apatopus*

Examination of Triassic footprints from every continent yields nothing similar enough to *Apatopus* to justify comparison in terms of footprint taxonomy. We may more profitably investigate the nature and systematic position of the trackmaker. In its foot structure and body proportions *Apatopus* shows closest affinities to quadrupedal members of the Subclass Archosauria — i.e. the Phytosauria, Pseudosuchia and Crocodilia. These groups will be considered in reverse sequence, beginning with the best known.

Locomotion in crocodiles, which has been investigated by Abel (1912, p. 217), Huene (1913), and Schaeffer (1941, p. 443 ff.), is of three types: a slow, lizard-like dragging of the body, a spring in which all four feet thrust simultaneously, and a striding gait in which the belly is well above the ground and only the tail-tip leaves a mark. Of these gaits only the last would produce trackways comparable to that of *Apatopus*; thus neither the "Gehspur" nor the "Laufspur" which Huene figures is pertinent to this discussion. An example of the true striding gait in a juvenile *Alligator mississippiensis* has been recorded on film by Schaeffer. The resulting trackway shows a pace angulation of only 80°, i.e. the stride is little longer than the pace. In evaluating this record the smallness of the alligator and the



Fig. 8. Type trackway of *Apatopus lineatus* (Bock) with third manus-pes set added and footprints somewhat restored, x 1/6. Lafayette College S490 plus MCZ 212.

fact that it was walking on glass must be considered. For example, the 20° to 30° outward rotation of the pes between implantation and withdrawal can hardly be normal: no such rotation is evident in the alligator trackway figured by Jaeger (1948, pl. 170 c), and only in very muddy footing did the pes of *Apatopus* rotate a few degrees outward (cf. Plate 4, figure 2). I believe that on a fairly firm surface a crocodilian in rapid motion would produce a trackway rather similar in proportions to that of *Apatopus*. We have already noted the crocodilian habitus indicated by the aquatic adaptations in the feet of the Milford trackmaker.

Despite these similarities in habitus *Apatopus* can hardly have been a crocodilian by heritage. The ancestral crocodilian *Protosuchus* from Upper Triassic or Lower Jurassic beds of Arizona had already developed an essentially modern type of foot with an elongate metatarsus, reduced fourth and rudimentary fifth digits, and a formula of 2-3-4-4-0 (Colbert and Mook, 1951). These characteristics were probably inherited without much modification from pseudosuchian ancestors and have been transmitted without much modification to the living crocodilians. Even the aberrant pes structure in the marine thalattosuchians can be more readily derived from the *Protosuchus* pattern than could that of *Apatopus*. Another point of distinction is the out-turned manus which characterizes crocodilian trackways. Thus the Milford trackmaker cannot be referred to any crocodilian lineage.

Among trackways which have been ascribed to pseudosuchians certain members of the *Batrachopus* group approach the *Apatopus* pattern. Nevertheless the reconstructed feet of these forms — and the few known pseudosuchian foot skeletons — are distinctly different, particularly in the fourth and fifth pes digits.

In the Phytosauria we find the logical correlative for a trackmaker which is crocodilian in body form and presumed habitus but not in skeletal structure. The comparative proportions of the crocodilians *Gavialis*, *Tomistoma* and *Alligator*, and the phytosaurs *Rutiodon*, *Machaeroprotopus* and *Mystriosuchus* have been analyzed by Colbert (1947), who attests to the remarkable parallelism noted by earlier authors. Very little articulated phytosaurian foot material, unfortunately, is available for comparison with the footprints. The manus is best represented

in *Mystriosuchus* (McGregor, 1906, fig. 10), in which — like *Apatopus* — the metacarpal bundle is nearly bilaterally symmetrical and digit V bears three phalanges which are about twice as long as they are wide. Further comparisons cannot be made. McGregor's reconstruction of the pes in *Rutiodon*, based on incomplete, scattered material of several individuals, is remarkably similar to my restoration of *Apatopus* — which (except where drawn in dashed lines) was quite independently derived from the footprints alone. If *Apatopus* is indeed a phytosaur, then Dr. McGregor proves to have been indeed a prophet worthy of honor.

Correlation with the Phytosauria is supported by all the evidence and contradicted by none; it may therefore be taken as a working assumption. Possible equivalents exist in the two phytosaurs of the Newark series, *Rutiodon* and *Clepsysaurus* (?=*Machaeroprotopus*). The significant differences in skeletal proportions between these genera would presumably be reflected in their trackways and may someday permit positive assignment of *Apatopus lineatus* to one or the other. Present knowledge, however, does not justify comparison of the single, partial *Apatopus* trackway with the composite skeleton of *Rutiodon* from North Carolina (Colbert, 1947) as opposed to incomplete skeletons from Arizona which may be congeneric with *Clepsysaurus* (Camp, 1930). Geographic distribution of the Newark phytosaurs offers a possible guide to the identity of *A. lineatus*, for Colbert and Chaffee (1941) concur with Camp's conclusion that all the phytosaur remains from Pennsylvania, New Jersey, and Connecticut represent *Clepsysaurus* while the North Carolina finds all pertain to *Rutiodon*.<sup>6</sup> *Apatopus lineatus* would thus appear to be a correlative of *Clepsysaurus*.

So far as I know these Milford specimens are the only phytosaur footprints yet described.<sup>7</sup> Paradoxically, phytosaur bones are the commonest skeletal remains of both the Chinle formation of the Southwest and the Newark series of the East (excluding,

<sup>6</sup> H. E. Wanner's (1926) specimens of "*Rutiodon carolinensis*" from the Newark series of York County, Pennsylvania — overlooked by the above-mentioned authors and by the Hay-Camp bibliographies — merit further study.

<sup>7</sup> An isolated pes imprint, considered by Bock (1952, pl. 46, fig. 2) to be probably that of a large parasuchian of the *Clepsysaurus* type, bears no resemblance to *Apatopus*. So far as its preservation permits comparisons, it seems more similar to ornithoid footprints of the *Plectropterna* type from the Connecticut Valley.

significantly, the Meriden and Portland formations). In the ecology lies the probable explanation for this discrepancy: Triassic footprint assemblages as a rule represent terrestrial faunas while the fossil deposits contain a disproportionate number of aquatic forms. Thus the presence of several phytosaurs in a dinosaur-pseudosuchian-lacertoid footprint faunule at Milford is rather anomalous.

## REPTILIA LACERTOIDEA INCERTAE SEDIS

### Genus RHYNCHOSAUIROIDES Beasley *in* Maidwell, 1911

*Pontopus* Nopces, 1923, p. 141. Keuper of England.

*Akropus* Rühle von Lilienstern, 1939, p. 298. Bunter of Germany; Moenkopi of Arizona (Peabody, 1948, p. 319 ff.).

*Hamatopus* Rühle von Lilienstern, 1939, p. 319. Bunter of Germany.

*Rhynchocephalichnus* Huene, 1941, p. 14. Keuper (Verrucano) of Italy; Keuper of Germany (Heller, 1956).

*Eurichnus* Lull, 1942A, p. 502; Branson, 1947, p. 590. Lower Triassic (Chugwater) of Wyoming.

The type species is here designated as *R. rectipes* Beasley *in* Maidwell, the type specimen of which is a manus-pes set from the Keuper of Daresbury, England (Dr. Ricketts' collection, University of Liverpool Geology Department).

### RHYNCHOSAUIROIDES HYPERBATES Baird, n. sp.

#### Figures 9 A, 10

*Type.* ANS 15210, a trackway of one pes and three manus imprints associated with the type of *Chirotherium* "*copei*."

*Hypodigm.* The type; an isolated left pes on the same slab; MCZ 210, a partial left pes associated with *C. parvum*.

*Diagnosis.* Manus broad with little disparity in digit lengths; gait digitigrade with hallux non-functional and proximal ends of proximal phalanges normally carried clear of the ground. The specific name alludes to the overstepping of manus by pes.

*Morphology.* The trackway is rather narrow, showing a stride of 44 cm., forelimb paces of 23 and 25.5 cm., and a pace angulation of 130° between manus imprints. (In these measurements a 3-cm. fissure filling which crosses the trackway is ignored, as the relative ages of trackway and fissure are unknown.) As in



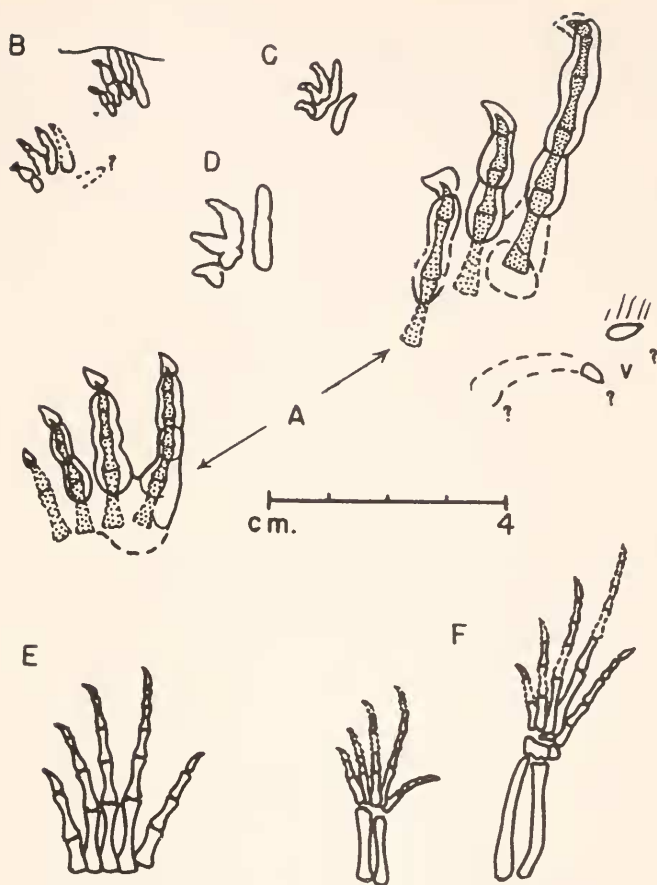


Fig. 9. A. *Rhynchosauroides hyperbates* n. sp., composite restoration of manus (at left) and pes in normal position. B-C. Small *Rhynchosauroides* footprints from Milford: B, (ANS 15210); C, manus imprint (MCZ 213). D. Manus imprint from Trostle quarry near York Springs, Adams Co., Pa. (Carnegie Museum 12082). E. Manus of *Monjurosuchus* reconstructed from Endo's photograph. F. Manus and pes of *Polysphenodon mülleri* Jaekel, modified from Huene. All  $\times 4/5$ .



Fig. 10. Type trackway of *Rhynchosauroides hyperbates* n. sp. (ANS 15210), x 1/5, with trackmaker restored as a sphenodontid rhynchocephalian. First manus-pes set and left pes added, fifth digits hypothetical. Footprints of *Chirotherium parvum* (*C. "copci"* type) in dashed outline.

other Triassic lacertoid trackways the pes is strongly out-turned and evidently overstepped the manus as it implanted.<sup>8</sup> The trackmaker, which is restored in walking pose in Figure 10, had a gleno-acetabular length of about 18 cm. and a total length of perhaps 75 cm.

The foot structure, revealed by comparing outlines printed from latex molds of all the imprints, is decidedly lacertoid. Well-developed articular swellings indicate an apparent phalangeal formula of 1-2-3-4-? in the manus and ?-2-3-4-? in the pes. This formula must be incomplete, for the obvious reptilian character of the feet connotes a normal formula of 2-3-4-5-3(4). Like the structurally similar Moenkopi genus *Rotodactylus* (Peabody, 1948, p. 329), the Milford form must have been digitigrade to such an extent that each proximal phalanx was elevated with its metapodial; normally only the padded distal articulation of phalanx 1 touched the ground. All the digits recorded bear sharp claws, either extended or curved toward the trackway midline.

The pollex is represented only by claw impressions. Nothing which can be identified as the imprint of a fifth manus digit is visible. The absence of any hallux imprint and the disparity in length of the pes digits indicate that the hallux was non-functional. Pes digit V has left no unequivocal record, but obscure marks on MCZ 210 and ANS 15210 may have been made by a lacertoid, laterally projecting minimus. Both these marks are shown, for what they may be worth, in Figure 9 A.

#### RHYNCHOSAUIROIDES SP.

##### Figure 9 B, C; Plate 3, Figure 2

A pair of minute footprints on the ANS slab, unfortunately too incomplete for reliable analysis, and indistinct trackways of comparable size on a slab with *Apatopus lineatus* (MCZ 213) prove the presence of another species of *Rhynchosauiroides* in the Level B faunule. Smaller size and greater disparity in the lengths of the manus digits distinguish it from *R. hyperbates*.

<sup>8</sup>I have seen no evidence in Pennsylvanian, Permian, or Triassic lacertoid trackways that the pes rotated nearly 90° outward during the propulsive phase as Schaeffer (1941, p. 449) has observed in experiments with *Anolis*. Except for an occasional rotational slippage of a few degrees in unusually soft mud the pes remained in implantation position until withdrawn.

## Relationships

Lacertoid trackways of this sort are familiar companions of *Chirotherium* in the Lower and Upper Triassic of both Europe and America. As indicated in the synonymy, a number of generic names have been applied to them. The differences between these nominal genera are, however, slight: for example, Rühle von Lilienstern distinguished *Hamatopus* from *Akropus* largely by the more hooked appearance of its digit tips. A more practical treatment here proposed is to consider these forms as species of a single form-genus *Rhynchosauroides* which is comparable to *Chirotherium* in its range of variation. This form-genus, of cosmopolitan distribution in continental Triassic beds, undoubtedly represents several reptilian genera; but until more is known of Triassic lacertoid feet and footprints there seems little advantage in proliferating form-genera on differences of uncertain diagnostic value.

Our lack of data on the fifth digits of manus and pes hinders comparison of *Rhynchosauroides hyperbates* to other species. Its closest similarities, however, are to the footprints from the English Keuper which were described by Beasley (1905) and comprehensively reviewed by Maidwell (1911, 1914). The smaller Milford lacertoid is less similar to the larger one than to *Rhynchosauroides* [*Rhynchocephalichnus*] *franconicus* (Heller, 1956; see also Haarländer, 1938) from the Keuper of Germany.

Such trackways have never been found in the well-known footprint faunas of Portland and Meriden age in the Connecticut valley, though they are not uncommon in the Brunswick and Lockatong formations of the Pennsylvania-New Jersey basin. The Milford forms cannot adequately be compared with *Rhynchosauroides* ["*Orthodactylus*"]<sup>9</sup> *howelli* (Bock) from an earlier horizon of the Brunswick near Schwenkville, Pennsylvania, until better-preserved material is available. An isolated *Rhyncho-*

<sup>9</sup> This form has nothing to do with Hitchcock's *Orthodactylus* from the Portland formation of Gill, Massachusetts. The type specimen of the type species *O. floriferus* is an obscurely recorded trackway of pseudosuchian or proto-crocodilian type, having the manus anterior to the pes and strongly out-turned as in the contemporary *Chirotheroides*. Superficial similarity of the digital gouge-marks apparently prompted Bock (1952, p. 421) to refer his Schwenkville tracks and some Lower Permian "Schwimmispuren" (Schmidtgen, 1927, fig. 3) to *Orthodactylus*. On the other hand, Triassic "Schwimmispuren" similar to Schmidtgen's and equally indeterminate were made the type of a new species, *Procolophonipus conhuenei* Bock (p. 419), ascribed to a plump, slow-moving reptile which jumped quadrupedally without leaving manus imprints.

*sauroides* manus imprint of Brunswick age from the Trostle stone quarry near York Springs, Adams County, Pennsylvania, is shown in Figure 9 D; and another of Lockatong age from Phoenixville, Pennsylvania, has been figured without name by Bock (1952, pl. 48, fig. 2). Aside from some undescribed trackways from the Dockum group of the Cimarron Valley in north-eastern New Mexico (AMNH 6338), these are the only records of *Rhynchosauroides* in the Upper Triassic of North America.

The systematic position of the trackmakers is debatable. Footprints of this sort have been referred by various authors to the Protorosauria, Eosuchia, Pseudosuchia, Rhynchocephalia and Lacertilia; and indeed each of these groups has Triassic representatives which would have made lacertoid footprints. Among the Protorosauria the tanystropheid *Macrocnemus* from the Alpine Middle Triassic (Peyer, 1937) is similar in size and proportions. Its reduced fifth digits of manus and pes exclude it from correlation with the European species of *Rhynchosauroides*, and its greater disparity in the lengths of the manus digits distinguishes it from the larger Milford form. A similar disparity characterizes the manus of *Trilophosaurus* from the Upper Triassic (Dockum) of Texas (Gregory, 1945); but its pes digits are much less unequal in length. The proximal end of ungual II lies opposite those of phalanges III-3 and IV-2, while in the footprints it lies opposite the proximal end of III-2 and the waist of IV-1, much as in the Permian *Protorosaurus*. But as the known Triassic protorosaurian genera undoubtedly constitute only a fraction of the number that once lived, the group cannot be disregarded as a possible source of Keuper lacertoid trackways.

Too little is known of limb structure in the Eosuchia to permit useful comparison.

Peabody (1948, p. 337) has referred his Lower Triassic footprint genus *Rotodactylus* to the Pseudosuchia on the basis of its long-striding gait with pendulum limb movement, its semi-bipedal concentration of the body weight on the long hind limbs, and its digitigrade pes with posteriorly rotated, prop-like fifth digit. Isolated manus-pes sets of *Rotodactylus* appear deceptively lacertoid (especially where the fifth digit has failed to impress), but the whole organization of the animal is significantly

different from that of lizard-like reptiles.<sup>10</sup> Aside from its overstepping gait and similar digitigrade specialization the Milford trackmaker appears to be basically unlike *Rotodactylus*. No comparable pseudosuchian skeleton is known.

The case for the Rhynchocephalia as a source for Triassic lacertoid footprints, reviewed by Huene (1938, 1941) and Peabody (1948), dates historically from Richard Owen, who in 1842 assigned the small footprints of the Grinsill quarries near Shrewsbury to *Rhynchosaurus articeps* on the grounds that the bones and footprints correspond in size and occur in the same beds, to the exclusion of other bones and footprints. This correlation was accepted by subsequent students of British Keuper footprints and indeed motivated Beasley to coin the name *Rhynchosauroides*.

A basic similarity certainly exists between *Rhynchosauroides* footprints and the feet of *Rhynchosaurus* as restored by Smith Woodward (1907). But closer inspection shows that nearly all the footprints were made by long-legged, slender-toed reptiles, whereas *Rhynchosaurus* is comparatively short-legged and broad-toed as a modification for aquatic life. At this point it may be illuminating to note that in the same year in which he proposed the *Rhynchosaurus* correlation Owen was asserting, on essentially similar grounds, that *Chirotherium* footprints represented *Labyrinthodon*. The great contrast (now understood) between the feeble-limbed, bottom-crawling "*Labyrinthodon*" and the up-right-limbed, semi-cursorial *Chirotherium* points up the ecological unsoundness of both correlations: the genera common in the Keuper bonebeds represent an aquatic facies-fauna while the footprints record a terrestrial facies-fauna.

Among terrestrial rhynchocephalians we may eliminate the Rhynchosauridae because of their un-lacertoid proportions and short, heavy phalanges. The Sphenodontidae, however, offer closer comparisons. Proportions similar to those of the Milford trackmaker are found in the Upper Jurassic *Homocosaurus*; the Manchurian sphenodontid *Monjurosuchus* (Endo, 1940) is rather similar in manus structure (Figure 9 E) although its body proportions suggest that the pes probably did not overstep the

<sup>10</sup> Bock's attempt (1952, p. 422) to synonymize *Rotodactylus* with the araeosceloid Lower Permian footprint "*Ichnium gampsodactylum*" — more correctly termed *Dromopus* [*Saurichnites*] *lacertoides* (Geinitz), n. comb. — overvalues the apparent similarities at the expense of fundamental differences in foot structure and trackway pattern.



manus as much as in *Rhynchosauroides hyperbates*. Upper Triassic genera are (at this writing) less completely known, but the limbs of *Polysphenodon* compare favorably (as Huene points out) with footprints of the *Rhynchosauroides* type from the Keuper of Italy. As shown in Figure 9 F, the phalangeal pattern of *Polysphenodon* also corresponds approximately to that of the larger Milford lacertoid. The publication of current research on several skeletons of *Glevosaurus*, a sphenodontid from Keuper fissure fillings in Gloucestershire (Robinson, 1955), may well provide the means to a better understanding of *Rhynchosauroides*.

Triassic Lacertilia, a group in which major advances in knowledge are in progress, may similarly prove to correlate with some of the lacertoid trackways which I have brigaded under the name *Rhynchosauroides*. On the evidence now available *R. hyperbates* is assigned tentatively to the sphenodontid Rhynchocephalia, but lacertilian origin remains a distinct possibility. At present the various trackways cited above constitute the only evidence of rhynchocephalians or lacertilians in the North American Triassic.

### CORRELATIVE AGE OF THE MILFORD FAUNULES

Research on several problems of Pennsylvanian and Permian ichnology, still unpublished, indicates that fossil footprints—especially footprint faunas—can be used in a limited way for stratigraphic correlation. As footprint species can at best be equated only with generic units of tetrapods they cannot approach the diagnostic precision of skeletal remains. Assemblages of footprints are of course subject to the same ecological bias as assemblages of skeletons, and may be equally deceptive in suggesting the non-contemporaneity of beds which are actually equivalent in age.

Despite such limitations ichnological evidence can be a valid basis for correlation; indeed, it is sometimes the only basis available. One pertinent example is the presence of similar *Chirotherium barthii* faunas in the Bunter of Germany and the Moenkopi of Arizona, which (with other evidence) establishes the equivalence of these strata. Consequently when a specimen of *C. barthii* which is indistinguishable from the Arizona ma-

terial appears (under the name "*C. higuereensis*") in so-called Upper Permian beds of Argentina (Rusconi, 1951) we need feel no doubt that the beds are in fact Triassic.<sup>11</sup>

The amount of material now available and the size and diversity of the combined Milford faunules justifies an attempt at correlating them with faunas of other areas. In this assay footprints will be compared with footprints and bones with bones: for in the past, uncritical herpetological interpretations of misidentified and unanalyzed footprints have too often proved misleading in stratigraphic work.

Two views on the correlative age of the Milford footprints have been advanced: one, that the footprint assemblages of Milford and Whitehall, New Jersey, York Springs, Pennsylvania, and Aldie, Virginia, compare closely with the youngest footprint fauna of the Portland formation in Massachusetts (Boek, 1952, pp. 429-430); the other, that the Milford faunules correlate neither with the Portland nor the underlying Meriden but with the New Haven, lowermost of the Connecticut Valley formations (Baird, 1954, pp. 184-187). Let us examine these faunules, beginning with the southernmost.

The only specimen from Aldie available to me (MCZ 236) is a well-preserved pes imprint, 35 cm. long including the hallux, of *Anchisauripus tuberosus* (Hitchcock). This species ranges from the lower Meriden to the upper Portland formation. Of the Aldie fauna Gilmore (1924) says:

"Three-toed imprints predominate though they vary in size from a length of three to fourteen inches. A few tracks were noticed having four toes, evidently terminated with wide, flat unguals. All of these are probably of dinosaurian origin, but a few small 4- or 5-toed tracks with traces of sharp claws perhaps pertain to some other group."

Until this important assemblage has been thoroughly studied no valid comparisons can be made.

Specimens from the Gettysburg shale of the Trostle stone quarry near York Springs, Adams County, Pennsylvania, are figured by Stose and Jonas (1939, pl. 22); others are preserved at the Carnegie Museum. In addition to invertebrate trackways

<sup>11</sup> Since the foregoing was written Peabody (1955) has published the same observation and noted the importance of this evidence on Triassic faunal distribution.

and some indeterminate vertebrate tracks the faunule contains three genera: (1) a uniquely quadrupedal dinosaurian type resembling *Anchisauripus gwyneddensis* Bock from the Lockatong formation, (2) a *Rhynchosauroides* (Figure 9 D) comparable to those from the Brunswick of Schwenkville and Milford and the Lockatong of Phoenixville, and (3) large footprints consisting of a sub-circular plantar pad close behind an arc of broad ungual depressions, rather suggestive of a dicynodont foot. Nothing like any of these forms occurs in the Connecticut Valley.

The Whitehall footprints are known to me only from the thoroughly unreliable faunal list of C. H. Hitchcock (1889). Further discussion is useless until the material can be restudied by modern methods.

Only one of the Milford species, *Anchisauripus parallelus*, also occurs in the Connecticut Valley. The other dinosaurian tracks are distinctly different from those of the Meriden and Portland formations. *Chirotherium* footprints, which at Milford record three genera of pseudosuchian reptiles, are unknown in New England; so are trackways of the *Apatopus* and *Rhynchosauroides* types. Their absence there is real and cannot be explained as the result of inadequate collecting or superficial study — far from it! In the absence of any evidence of barriers between the New Jersey-Pennsylvania basin and the ancient Connecticut Valley trough, the conclusion presented in my previous paper seems inescapable: the footprint beds of the upper Brunswick formation at Milford, New Jersey, antedate the Portland and Meriden formations and more probably correlate with the New Haven arkose of Connecticut. The most comparable footprints in the European sequence occur in formations of the middle to upper Middle Keuper of Germany.

## REPTILES OF THE BRUNSWICK FORMATION

To recapitulate, the Milford footprints comprise three mutually exclusive faunules from three horizons of the Brunswick formation. What these footprints signify in herpetological terms is summarized, so far as known, in Table 3. These footprints probably represent only a few of the different types of reptiles which inhabited the area, and the reptiles themselves only a segment of the biota. Nevertheless a partial account of the

TABLE 3  
MILFORD FOOTPRINT FAUNULES WITH PRESUMED REPTILIAN EQUIVALENTS

HORIZON	SPECIES	INTERPRETATION	INDIVIDUALS
Reddish-brown siltstone	<i>Chirotherium lulli</i>	Small ornithosuchid pseudosuchian, cf. <i>Euparkeria</i>	1
	cf. <i>Coelurosaurichnus</i>	Small coelurosaur or ?tridactyl pseudosuchian	1
	cf. <i>Anchisauripus gwyneddensis</i>	Small dinosaur	1
Level A	<i>Grallator sulcatus</i> , n. sp.	Coelurosaur, cf. <i>Coelophysis</i>	Several
Level B	<i>Anchisauripus milfordensis</i>	Coelurosaur	3+
Gray shale & sandstone at Levels A and B	<i>Anchisauripus parallelus</i>	Coelurosaur	1
	Genus incertum	Small dinosaur	1
	<i>Chirotherium parvum</i>	Large pseudosuchian	3
	<i>Chirotherium eyermani</i> , n. sp.	Large pseudosuchian	1
	<i>Apatopus lineatus</i> , n. gen.	Phytosaur, cf. <i>Clepsysaurus</i>	5-6
	<i>Rhynchosauroides hyperbates</i> , n. sp.; <i>R.</i> sp.	Sphenodontid rhynchocephalians or lacertilians	2, 3+

Brunswick fauna and its ecological relationships can be formulated from the known footprints and bones.

*Faunal content.* In the preceding attempts to determine the zoological positions of the trackmakers, failure to achieve a correlation between footprint and reptile has been due less often to inadequacy of the footprint material than to lack of comparable skeletal material. This lack is twofold in origin. First, the Triassic reptiles as known are largely a spectral crew of footless bodies and disembodied heads which can be made whole only by persistent and lucky collecting. As our knowledge of these forms increases, closer comparisons with the tracks will no doubt become possible. Second, and more fundamental than the fragmentary preservation of individual taxa, is the fragmentary and selective preservation of the original fauna. At present we know more types of Brunswick tetrapods from their footprints than from skeletal material. Aside from a dinosaur leg excavated by laborers but never collected (Colbert, 1946, p. 231), the only genera known are the metoposaurid amphibian *Eupelor*, the procolophonid cotylosaur *Hypsognathus*, the phytosaur *Clepsysaurus*, and the aëtosaurid pseudosuchian *Stegomus*.

Other Brunswick footprint assemblages — e.g. from Sanatoga and Collegeville, Pennsylvania, and Tumble Falls and Whitehall, New Jersey — which would augment the fauna have been omitted here because of the unreliability of old identifications. Figured specimens of *Anchisauripus* ["*Otouphepus*"] *poolei* (Bock) and *Rhynchosauroides* ["*Orthodactylus*"] *howelli* (Bock) from Schwenkville, Pennsylvania, which Wilhelm Bock has kindly made available for study are specifically indeterminate but appear to record a coelurosaur and a lacertoid reptile of sphenodontid aspect. The Schwenkville "*Grallator cuneatus*" (Bock, 1952, pl. 45, fig. 1) is surely not that genus but instead has the phalangeal pattern of *Anchisauripus*; it evidently represents another variety of coelurosaur.

*Ecology.* The Brunswick fauna is predominantly terrestrial but includes representatives of the aquatic biotope in the form of metoposaurs and phytosaurs. These were certainly fish-eaters and presumably fed on the coelacanth, semionotids, dictyopygids and palaeoniscids of the Newark lakes and streams. The presumed sphenodontid rhynchocephalians of Level B may (like

*Homoeosaurus*) also have fed occasionally on fish, but the bulk of their diet (like that of *Sphenodon*) probably consisted of insects, other arthropods, grubs, and small tetrapods. Except for the cotylosaur *Hyposognathus*, a presumed herbivore, the other known members of the fauna were carnivorous. Lacertoids and procolophonids furnished food for small, agile pseudosuchians of the *Chirotherium lulli* type, and all three groups formed the prey of the raptorial coelurosaurs. Whether the larger Milford pseudosuchians were predators or carrion-feeders, or both, cannot yet be determined.

Any assessment of the Brunswick ecology must allow for a disproportionate percentage of aquatic animals in the skeletal record; the footprint horizons, on the other hand, record a more representative proportion of terrestrial genera. More important, the footprint faunules constitute biocoenoses in a strict sense, while the skeletal remains occur as isolated finds or (at best) as bonebed thanatocoenoses of animals which may or may not have formed natural communities in life. Thus we can say with confidence that the reptiles of Level B, for example, constituted an animal community which occupied the Milford mudflat during a period measured in days. Our sample is too small, unfortunately, to furnish significant data on the numerical composition of the faunules.

*Survey of the Newark tetrapods.* Undoubtedly the assemblage described above is only a fraction of the actual tetrapod fauna of Brunswick time. To afford a clearer perspective, the known terrestrial vertebrates of the entire Newark province are listed with the Milford trackmakers in Table 4.

How incomplete this faunal picture remains may be deduced from the many reptiles and amphibians, both genera and higher groups, which are known from the Upper Triassic of Arizona, Utah, New Mexico, Texas and Wyoming. Among these are the metoposaurid amphibian *Eupelor* [= *Buettneria*, etc.] (Colbert and Imbrie, 1956), the large protorosaur *Trilophosaurus*, a variety of phytosaurs, the armor-plated pseudosuchians *Desmatosuchus* and *Typothorax*, the little ornithosuchid pseudosuchian *Hesperosuchus*, the coelurosaur *Coelophys*, and the dicynodont *Placerias*. Many of these forms (or their relatives) must have inhabited the Newark depositional area. Still other types of



tetrapods yet unknown, small forms in particular, completed the fauna.

It would obviously be premature to attempt here a reconstruction of late Triassic tetrapod faunas in space and time on the basis of skeletal and ichnological data now available. This is a major project to which several researchers are individually contributing, and in which the collaboration of invertebrate paleontologists, paleobotanists, and geologists is essential. Nevertheless the present study may serve to illustrate the contribution which one field of investigation, ichnology, can make to the solution of the general problem.

---

#### APPENDIX I: THE NATURE OF OTOUPHEPUS

A study of the type specimen of *Otouphepus magnificus* Cushman, lent through the courtesy of the Museum of Science, Boston, suggests that it is not the direct imprint of a foot but rather an impression transmitted to a surface some millimeters below the one on which the animal walked. This circumstance has softened the outlines and produced the illusion of a compact foot in which the digits were firmly united and surrounded by a web. The dark-colored web outline described by Cushman (1904, p. 155) proves to be a thin coat of gum which was readily removed with soap and water. Analysis of the pattern of articular pads reveals a pedal structure which is well within the limits of *Anchisauripus*. A previously undescribed claw-mark occupies exactly the position of an *Anchisauripus* hallux imprint.

The only plesiotype cited by number (Lull, 1953, p. 177) is morphologically indistinguishable from *Anchisaurus tuberosus* — a fact which Lull has pointed out in recent correspondence.

In size and skeletal structure the unique specimen of *O. minor* Lull (1915, p. 190) is a typical *Grallator*; its peculiarities are readily explained as artifacts of impression. (Latex molds of the two preceding specimens were kindly furnished by the Yale Peabody Museum.)

A third species, *O. poolei* Bock (1952, p. 407) has been based on an obscure and isolated footprint from the Brunswick formation near Schwenkville, Pennsylvania. With Wilhelm Bock's gracious permission this specimen has been latex-molded and

TAXA	SKELETAL REMAINS	MILFORD TRACKMAKERS (as genera) (B)
AMPHIBIA		
Stereospondyli:		
Metoposauridae	<i>Eupelor</i> [ <i>Calamops</i> ] (S, G) <i>Dictyocephalus</i> (DR)	
REPTILIA		
Cotylosauria:		
Procolophonidae	<i>Hypsognathus</i> (B)	
Rhynchocephalia (?)		2 isphenodontids
Pseudosuchia:		2 large pseudosuchians
Ornithosuchidae	<i>Stegomosuchus</i> (P)	1 ?+ ornithosuchid
Aëtosauridae	<i>Stegomus</i> (B, NH)	
Phytosauria	<i>Clepsysaurus</i> (L, B, G, PD, NH) <i>Rutiodon</i> (DR, ?G)	1 cf. <i>Clepsysaurus</i>
Coelurosauria:		3+ coelurosaurs
Ammosauridae	<i>Ammosaurus</i> (P)	
Podokesauridae	<i>Podokesaurus</i> (P)	1 cf. <i>Coelophys</i>
Prosauropoda:		
Thecodontosauridae	<i>Taleosaurus</i> (P) <i>Thecodontosaurus</i> (L, P)	
Cynodontia	<i>Dromatherium</i> (DR) <i>Microconodon</i> (DR)	
INCERTAE SEDIS	<i>Gwyneddosaurus</i> (L) <i>Lysorocephalus</i> (L)	

analyzed. An apparent structural formula of B, B, C, C allies this species with the *Anchisauripus tuberosus-exsertus-parallelus* species group. The species is probably distinct, but in the absence of adequate material its small size is the only characteristic which cannot be attributed to impression phenomena.

If *Otouphepus* Cushman (March, 1904) and *Anchisauripus* Lull (April, 1904) are synonymous the former takes priority. To abandon a well-established name which has been applied to several species comprising thousands of specimens, in favor of a name which has been applied to four specimens whose chief point of similarity is their obscurity, would be unreasonably legalistic. I have therefore (Baird, 1956) petitioned that the International Commission for Zoological Nomenclature exercise its plenary powers to suppress *Otouphepus magnificus* as a *nomen dubium*; this action automatically entails the suppression of Lull's family Otouphepodidae. At the same time *Anchisauripus sillimani* and the family name Anchisauripodidae are to be placed on the official lists of names in zoology as *nomina conservanda*.

## APPENDIX II: BRONTOZOOM

The generic name *Brontozoum*, formerly applied to a number of species of theropod footprints from the Newark series, was erroneously reduced to synonymy in Hay's 1902 bibliography. In his monograph of 1904 Lull followed Hay's usage, and since that time the name has been in disuse. *Brontozoum* nevertheless remains a valid prior generic name for the type species of *Anchisauripus* Lull, and could legally be revived to replace that well-known generic name. The facts are as follows:

*Brontozoum* Hitchcock, 1847, was proposed to include "five" species of which only three were cited by name: the new species

### TABLE 4. SURVEY OF THE NEWARK TETRAPODS

Formations: Deep River coal measures (**DR**) of North Carolina; Stockton (**S**), Lockatong (**L**), Brunswick (**B**) of Pennsylvania-New Jersey basin; Gettysburg shales (**G**) of York County, Pennsylvania (Wanner, 1926); bed below Palisades diabase (**PD**) of New Jersey; New Haven (**NH**), Meriden, Portland (**P**) of Connecticut Valley.

*parallelum*,<sup>12</sup> *sillimanium* (an invalid emendation of *sillimani*, 1843) and *giganteum*. No type species was designated. No subsequent author, to my knowledge, has designated a type species, so all three remain available.

A case of sorts could be made for the selection of *parallelum* through a broad construction of Article 30 A(a)(ii) of the International Rules of Zoological Nomenclature, which provides that the expression "n.g., n.sp.," can constitute a designation of type species. In this case such a construction is highly dubious, particularly as it cannot be claimed to represent the intent of the original author: for Hitchcock evidently had no intention of designating a type species for any of his footprint taxa. Furthermore, *parallelum* is based on two specimens — neither designated as type — which are not conspecific. My analysis assigns one of these (Hitchcock's fig. 2 b) to *Anchisauripus sillimani* and the other (fig. 2 a) to *Grallator tenuis*. To avoid confusion I designate the specimen represented by fig. 2 b as the type of *parallelum*, and reduce this species to subjective synonymy with *sillimani*.

The second species, *Brontozoum sillimani*, is the type species of *Anchisauripus* Lull, 1904 (see Baird, 1956, paragraph 6). Lull clearly erred in erecting a new genus with a type species for which the name *Brontozoum* was available.

The third species originally assigned to *Brontozoum*, *B. giganteum*, was first described by Hitchcock (1836) as a species of *Ornithichnites* and was later transferred by him to *Eubrontes* (1845) and to *Brontozoum* (1847). In 1902 Hay designated it as the type of *Eubrontes*.

Since according to Article 30 B(g)(i) of the International Rules the designation of a species as the type of one genus does not in itself preclude the selection of that species as the type of another genus, either *sillimani* or *giganteum* is eligible to be the type species of *Brontozoum*. If *sillimani* be selected then *Anchisauripus* (1904), an important name accepted for more than fifty years, must be replaced by *Brontozoum* (1847), a name generally rejected or ignored during the same period. If *giganteum* be selected, however, then *Brontozoum* becomes a

<sup>12</sup> This species *B. parallelum* is not to be confused with *Anchisauripus* [*Grallator*] *parallelus* (Hitchcock, 1865) although Hay (1902, p. 545) did so confuse it.

junior objective synonym of *Eubrontes* (1845) through the identity of their type species.

I therefore designate *Ornithichnites giganteus* Hitchcock, 1836, as type species of the nominal genus *Brontozoum*, thereby synonymizing that genus with *Eubrontes*. This suppression of *Brontozoum* serves to maintain the familiar nomenclature of Lull's classic monographs of 1915 and 1953 which have done so much to bring nomenclatural stability into a confused field.

### SUMMARY

*Problem and method.* Quarries in the Delaware valley near Milford, New Jersey, have yielded three faunules of reptile footprints at three horizons of the upper Brunswick formation (Newark series, Upper Triassic). Each determinable species was analyzed by comparison of outlines printed from latex molds of all adequately preserved specimens. Body proportions and locomotor habits of the trackmakers were deduced from trackways (where available) and the pedal skeletons were reconstructed from the arrangement of articular swellings in the footprints. Comparison with other Triassic footprints furnished data on faunal distribution and stratigraphic correlation; comparison of the restored skeletons with those of Triassic reptiles served to elucidate and enlarge the known Brunswick fauna.

*Reddish-brown siltstone layer.* The youngest faunule (discussed in a previous paper) records three reptilian genera as footprint species: an indeterminate small dinosaur, another resembling *Coelurosaurichnus* (sensu stricto) of the German Middle Keuper and the Gettysburg shale of Pennsylvania, and an ornithosuchid pseudosuchian, *Chirotherium lulli* Bock, the last-known member of its genus. This faunule and that of Level B are the only American *Chirotherium*-dinosaur associations known.

*Level A* (gray sandstone over shale). *Grallator sulcatus*, n. sp., a small dinosaur with digits II-III united and IV independent, is less digitigrade than its Connecticut Valley congeners. Among coelurosaurs the massive German *Halticosaurus* (as shown by pedal reconstruction) made footprints resembling *Eubrontes*; little *Procompsognathus* compares more closely with

*Grallator*, especially *G. cursorius*; and *Coelophys* correlates approximately with *G. sulcatus*.

*Level B* (gray sandstone over shale). Three dinosaur genera occur: *Anchisauripus milfordensis* (Bock), a broad-based footprint without functional hallux, found also in the Gettysburg shale of York County, Pennsylvania; *A. parallelus* (Hitchcock), only 6/11 the size of conspecific New England footprints; and an enigmatic small form of York County affinities. Taxonomic placement follows a new type of key based on relative positions of phalangeal and metatarsophalangeal joints. Re-analysis of various Upper Triassic theropod tracks by this method necessitates reassignment of several species and emphasizes the similarities between *Grallator* and *Anchisauripus* (sensu stricto), genera previously considered familially distinct but here united as Grallatoridae and correlated with coelurosaurian dinosaurs.

Two large chirotheriids with hoof-like fifth pes digits represent a lineage previously known only from the German Middle Keuper, here designated the brachychirotherian group. In *Chirotherium parvum* (C. H. Hitchcock) (= *C. copei* Bock), narrow claws on pes digits I-III were carried well above the distal pad and directed obliquely laterad; pes digit I was robust. In the new species *C. eyermani* straight, heavy claws I-IV lay at sole level and digit I was weak. Skeletal reconstructions of the large-manus *C. barthii* (cosmopolitan, Lower Triassic) and the small-manus *C. lomasi* (Keuper of England) contrast with those of the Milford brachychirotherians. All three Milford chirotheriids show parallel evolutionary tendencies — characteristic of late Triassic species — toward functional tetradactyly through elimination of lateral propping function in pes digit V. Inefficient locomotion and increased dinosaurian competition probably contributed to the extinction of *Chirotherium*. Pseudosuchians correlative with the large Milford species are unknown.

Discovery of additional material permits redescription of "*Otozoum*" *lineatus* Bock as a new type of footprint, *Apatopus* n. gen., correlated with a phytosaur such as *Clepsysaurus* — the first phytosaur footprints known. Crocodilian in trackway pattern except for the forward-turned manus, *Apatopus* differs from all crocodilians in its long fourth and functional fifth pes digits. Webs apparently connected the claw bases. Both adults



and juveniles are represented, one adult having a gleno-acetabular length of 52 cm.

Lacertoid footprints of the genus *Rhynchosauroides* [*Akropus*] occur in the Brunswick, Gettysburg, and Lockatong formations of Pennsylvania-New Jersey, the Dockum of New Mexico, and the Keuper of England and Italy. *Rhynchosauroides hyperbates*, n. sp., represents an agile reptile some 75 cm. long with a gleno-acetabular length of 18 cm. Pes regularly overstepped manus, and both were digitigrade with the metapodio-phalangeal joints carried clear of the ground. A smaller Milford species is inadequately known. Affinities appear to lie with the sphenodontid *Rhynchocephalia* or the *Lacertilia*.

*Correlative age.* The Milford faunules are akin to those of the Pennsylvania-New Jersey basin and the German middle to late Middle Keuper but not (as sometimes held) to the familiar footprint assemblages of the Portland and Meriden formations of New England. Only one of the dinosaurian species also occurs in the Connecticut Valley; while *Chirotherium*, *Apatopus*, and *Rhynchosauroides* are definitely absent from the abundant and thoroughly studied Portland and Meriden faunas. No topographic or ecologic barriers would seem to have prevented inter-regional migration. Presence of the phytosaur *Clepsysaurus* and the pseudosuchian *Stegomus* in the lowest formation (New Haven arkose) of the Connecticut Trias as well as in the Brunswick formation, and the possible correlation of the three episodes of igneous extrusion in New Jersey with the three lava flows of Meriden time, suggest that the Brunswick antedates the Portland. The Milford footprint beds of the upper Brunswick appear to correlate best with the New Haven arkose.

*Reptiles of the Brunswick formation.* Known skeletal remains include undetermined dinosaurs, the cotylosaur *Hypsognathus*, the aëtosaurid pseudosuchian *Stegomus*, and the phytosaur *Clepsysaurus*. To this fauna the Milford footprints add three or four types of coelurosaur, one small ornithosuchid and two large undetermined pseudosuchians, a phytosaur, and two lacertoids. From these combined faunal lists the ecological picture may at least be glimpsed, though only a fraction of the Brunswick fauna is yet known. The present study serves to illustrate the possible contribution of ichnology to the solution of Triassic faunal and stratigraphic problems.

*Appendix I.* The nominal genus *Otouphepus* proves to be a catch-all for obscurely preserved dinosaur footprints. Its suppression as a *nomen dubium* is proposed in order to prevent possible displacement of *Anchisauripus* as a junior synonym.

*Appendix II.* The long-disused name *Brontozoum* also threatens the stability of the later name *Anchisauripus*. *Brontozoum* is therefore cashiered by the designation of a type species which is also the type species of the earlier genus *Eubrontes*, so that the genera become objectively synonymous.

## REFERENCES

## ABEL, OTHENIO

1912. Grundzüge der Palaeobiologie der Wirbeltiere. Stuttgart: Schweizerbart, xv + 708 pp.

## BAIRD, DONALD

1954. *Chirotherium lulli*, a pseudosuchian reptile from New Jersey. Mus. Comp. Zool. Bull., vol. 111, pp. 163-192, 2 pls.
1956. Proposed use of the Plenary Powers (i) to protect the generic name *Anchisauripus* Lull, 1904, by suppressing the generic name *Otouphepus* Cushman, 1904, and (ii) to suppress the specific name *magnificus* Cushman, 1904, published in combination with the latter generic name (Class Reptilia: Theropoda [Ichnites]). Bull. Zool. Nomenclature, vol. 12, pp. 221-224.

## BEASLEY, H. C.

1905. Report on footprints from the Trias, Part II. British Assoc. Adv. Sci. Rept. for 1904, pp. 275-282, pls. 3-5.

## BEURLIN, KARL

1950. Neue Fährtenfunde aus der Fränkischen Trias. Neues Jahrb., Monatshefte (B), pp. 308-320.

## BOCK, WILHELM

1952. Triassic reptilian tracks and trends of locomotive evolution. Jour. Paleontology, vol. 26, pp. 395-433, pls. 41-50.
- 1952A. New eastern Triassic ginkgos. Wagner Free Inst. Sci. Bull., vol. 27, pp. 9-14, pl. 1.

## BRANSON, E. B.

1947. Triassic (Chugwater) footprints from Wyoming. Jour. Paleontology, vol. 21, pp. 588-590.

## CAMP, C. L.

1930. A study of the phytosaurs, with description of new material from western North America. Univ. California Mem., vol. 10, 161 pp., 6 pls.

## COLBERT, E. H.

1946. *Hypsognathus*, a Triassic reptile from New Jersey. Am. Mus. Nat. Hist. Bull., vol. 86, pp. 225-274, pls. 25-33.
1947. Studies of the phytosaurs *Machacroprosopus* and *Rutiodon*. Am. Mus. Nat. Hist. Bull., vol. 88, pp. 53-96, pls. 3-10.

## COLBERT, E. H., and R. G. CHAFFEE

1941. The type of *Clepsysaurus pennsylvanicus* and its bearing upon the genus *Rutiodon*. Acad. Nat. Sci. Philadelphia Notulae Naturae, no. 90, 19 pp.

## COLBERT, E. H., and JOHN IMBRIE

1956. Triassic metoposaurid amphibians. Am. Mus. Nat. Hist. Bull., vol. 110, pp. 399-452, pls. 25-28.

## COLBERT, E. H., and C. C. MOOK

1951. The ancestral crocodilian *Protosuchus*. Am. Mus. Nat. Hist. Bull., vol. 97, pp. 143-182, pls. 9-16.

## CUSHMAN, J. A.

1904. A new foot-print from the Connecticut valley. Am. Geologist, vol. 33, pp. 154-156, pl. 6.

## ENDO, RIUJI

1940. A new genus of Thecodontia from the Lycopoda beds in Manchoukuo. Central Nat. Mus. Manchoukuo Bull. 2, pp. 1-14, 2 pls.

## EYERMAN, JOHN

1886. Footprints on the Triassic sandstone (Jura-Trias) of New Jersey. Am. Jour. Sci., vol. 131, p. 72.
1889. Fossil foot-prints from the Jura(?) - Trias of New Jersey. Acad. Nat. Sci. Philadelphia Proc., pp. 32-33.

## GILMORE, C. W.

1924. Collecting fossil footprints in Virginia. Smithsonian Misc. Coll., vol. 76, pp. 16-18.

## GREGORY, J. T.

1945. Osteology and relationships of *Trilophosaurus*. Univ. Texas Pub. 4401, pp. 273-359, pls. 18-33.

GRIER, N. M.

1927. The Hitchcock lecture upon ichnology, and the Dartmouth College ichnological collection. *Am. Midland Nat.*, vol. 10, pp. 161-197.

HAARLÄNDER, WILHELM

1938. Bericht über einige Funde aus dem mittelfränkischen Keuper. Oberrhein. geol. Ver. Jahresber. (N. F.), Bd. 27, pp. 1-8, pls. 1-2.

HAY, O. P.

1902. Bibliography and catalogue of the fossil vertebrata of North America. *U. S. Geol. Survey Bull.* 179, 868 pp.

HEILMANN, GERHARD

1927. The origin of birds. New York: Appleton, vii + 210 pp.

HELLER, FLORIAN

1952. Reptilfährten-Funde aus dem Ansbacher Sandstein des Mittleren Keupers von Franken. *Geol. Blätt. NO-Bayern*, vol. 2, pp. 129-141, pl. 9.
1956. Rhynchocephalen-Fährten aus dem Mittleren Keuper bei Hassfurt am Main. *Ibid.*, vol. 6, pp. 50-55, pl. 2.

HICKOK, W. O. 4TH, and BRADFORD WILLARD

1933. Dinosaur foot tracks near Yocumtown, York County, Pennsylvania. *Pennsylvania Acad. Sci. Proc.*, vol. 7, pp. 55-58.

HITCHCOCK, C. H.

1889. Recent progress in ichnology. *Boston Soc. Nat. Hist. Proc.*, vol. 24, pp. 117-127.

HITCHCOCK, EDWARD

1836. Ornithichnology. Description of the footmarks of birds (*Ornithichnites*) on New Red sandstone in Massachusetts. *Am. Jour. Sci.*, vol. 29, pp. 307-340, 3 pls.
1843. Description of five new species of fossil footmarks, from the red sandstone of the valley of Connecticut River. *Assoc. Am. Geologists & Naturalists Trans.*, pp. 254-264, pl. 11.
1845. An attempt to name, classify and describe the animals that made the fossil footmarks of New England. *Assoc. Am. Geologists & Naturalists Proc.* 6th Ann. Meeting, pp. 23-25.
1847. Description of two new species of fossil footmarks found in Massachusetts and Connecticut, or of the animals that made them. *Am. Jour. Sci.* (2), vol. 4, pp. 46-57.

1858. *Ichnology of New England. A report on the sandstone of the Connecticut valley, especially its fossil footmarks.* Boston: Wm. White, 220 pp., 60 pls.
1865. *Supplement to the ichnology of New England.* Boston: Wright & Potter, x + 96 pp., 20 pls.

HUENE, FRIEDRICH VON

1913. Beobachtungen über die Bewegungsart der Extremitäten bei Krokodilen. *Biol. Centralbl.*, vol. 33, pp. 468-472.
1921. Neue Pseudosuchier und Coelurosaurier aus dem Württembergischen Keuper. *Acta Zoologica*, vol. 2, pp. 329-403, pls. 1-4.
1934. Ein neuer Coelurosaurier in der thüringischen Trias. *Palaeont. Zeitschr.*, vol. 16, pp. 145-170, pls. 13-16.
1938. Zur Bestimmung von Fussspuren der Protorosauriden und Rhynchosauriden. *Zentralbl. Mineralogie (B)*, no. 2, pp. 58-64.
1941. Die Tetrapoden-Fährten im toskanischen Verrucano und ihre Bedeutung. *Neues Jahrb., Beilage-Bd. 86 (B)*, pp. 1-34, pls. 1-8.
1944. Die fossilen Reptilien des südamerikanischen Gondwanalandes. München: C. H. Beck, viii + 332 pp., 38 pls.

JAEGER, ELLSWORTH

1948. *Tracks and trailcraft.* New York: Macmillan, x + 381 pp.

KAUP, J. J.

1835. Thier-Fährten von Hildburghausen: Chirotherium oder Chiro-saurus. *Neues Jahrb.*, pp. 327-328.

KUHN, OSKAR

1936. Weitere Parasuchier und Labyrinthodonten aus dem Blasen-stein des mittleren Keuper von Ebrach. *Palaeontographica*, vol. 83 (A), pp. 61-98, pls. 8-13.

LESLEY, J. P.

1889. *Dictionary of the fossils of Pennsylvania and neighboring states*, vol. 2. *Pennsylvania (2d) Geol. Survey Rept. P 4*, pp. 439-914 + i-x.

LULL, R. S.

1904. *Fossil footprints of the Jura-Trias of North America.* Boston Soc. Nat. Hist. Mem., vol. 5, pp. 461-557, pl. 72.
1915. *Triassic life of the Connecticut valley.* *Connecticut Geol. Nat. Hist. Survey Bull. 24*, 285 pp., 3 maps, 12 pls.
1917. *The Triassic fauna and flora of the Connecticut Valley.* *U. S. Geol. Survey Bull. 597*, pp. 105-127, pls. 3-4.
1942. *Triassic footprints from Argentina.* *Am. Jour. Sci.*, vol. 240, pp. 421-425, pl. 1.

- 1942A. Chugwater footprints from Wyoming. *Am. Jour. Sci.*, vol. 240, pp. 500-504.
1953. Triassic life of the Connecticut Valley (revised). Connecticut Geol. Nat. Hist. Survey Bull. 81, 331 pp.
- LYMAN, B. S.
1894. Some New Red horizons. *Am. Philos. Soc. Proc.*, vol. 33, pp. 192-215.
1895. Report on the New Red of Bucks and Montgomery Counties. Pennsylvania (2d) Geol. Survey Summary Final Rept., vol. 3, pt. 2, pp. i-iii + 2589-2638, pls. 596-611.
- MAIDWELL, F. T.
1911. Notes on footprints from the Keuper of Runcorn Hill. Liverpool Geol. Soc. Proc., vol. 11, pp. 140-152, pls. 4-6.
1914. Notes on footprints from the Keuper, II. Liverpool Geol. Soc. Proc., vol. 12, pp. 53-71, pls. 3-5.
- MCGREGOR, J. H.
1906. The Phytosauria, with especial reference to *Mystriosuchus* and *Rhytidodon*. *Am. Mus. Nat. Hist. Mem.*, vol. 9, pp. 27-101, pls. 6-11.
- NOPCSA, FRANZ
1923. Die Familien der Reptilien. *Fortschr. Geologie u. Palaeontologie*, vol. 2, pp. 1-210, pls. 1-6.
- OWEN, RICHARD
1842. Description of an extinct lacertian reptile, *Rhynchosaurus articeps* (Owen), of which the bones and foot-prints characterize the upper New Red sandstone at Grinsill, near Shrewsbury. Cambridge Philos. Soc. Trans., vol. 7, pp. 355-369, pls. 5-6.
- 1842A. Description of parts of the skeleton and teeth of five species of the genus *Labyrinthodon* . . . with remarks on the probable identity of the *Cheirotherium* with this genus of extinct Batrachians. *Geol. Soc. London Trans. (2)*, vol. 6, pp. 515-543, pls. 43-47.
- PEABODY, F. E.
1948. Reptile and amphibian trackways from the Lower Triassic Moenkopi formation of Arizona and Utah. *Univ. Calif. Dept. Geol. Sci. Bull.*, vol. 27, pp. 295-468, pls. 23-45.
1955. Occurrence of *Chirotherium* in South America. *Geol. Soc. Am. Bull.*, vol. 66, pp. 239-240.



## PEYER, BERNHARD

1937. Die Triasfauna der Tessiner Kalkalpen, XII. *Macrocnemus bassanii* Nopcsa. Schweizer. Palaeont. Gesell. Abh., vol. 59, pp. 1-140, pls. 55-63.

## RICHARDS, H. G.

1953. Record of the rocks. New York: Ronald Press, xiii + 413 pp.

## ROBINSON, P. L.

1955. Specimens of Triassic reptiles obtained from fissures in the Slickstones quarry, Gloucestershire. Geol. Soc. London Proc., No. 1527, pp. 113-115.

## RÜHLE VON LILIENSTERN, HUGO

1938. Fährten aus dem Blasensandstein (km 4 zeta) des mittleren Keupers von Südthüringen. Neues Jahrbuch, Beilage-Bd. 80 (B), pp. 63-71, pls. 2-3.
1939. Fährten und Spuren im Chirotheriumsandstein von Südthüringen. Fortschr. Geologie u. Palaeontologie, vol. 12, pp. i-iv + 293-387, pls. 1-12.

## RUSCONI, CARLOS

1951. Rastros de patas de reptiles pérmicos de Mendoza. Soc. Hist. Geog. Cuyo Rev., vol. 3, no. 3, pp. 1-14.

## SAWIN, H. J.

1947. The pseudosuchian reptile *Typothorax meadi*, new species. Jour. Paleontology, vol. 21, pp. 201-238, pl. 34.

## SCHAEFFER, BOBB

1941. The morphological and functional evolution of the tarsus in amphibians and reptiles. Am. Mus. Nat. Hist. Bull., vol. 78, pp. 395-472.

## SCHMIDTGEN, OTTO

1927. Tierfährten im oberen Rotliegenden bei Mainz. Palaeont. Zeitschr., vol. 9, pp. 101-107.

## SHIKAMA, TOKIO

1942. Footprints from Chinchou, Manchoukuo, of *Jeholosauripus*, the Eo-Mesozoic dinosaur. Central Nat. Mus. Manchoukuo Bull., no. 3, pp. 21-31, pls. 10-15.

## SOERGEL, WOLFGANG

1925. Die Fährten der Chirotheria. Eine paläobiologische Studie. Jena: G. Fischer, vii + 92 pp.

STOSE, G. W., and A. I. JONAS

1939. Geology and mineral resources of York County, Pennsylvania. Pennsylvania Geol. Survey (4), Bull. C 67, 199 pp., map.

VON ENGELN, O. D., and K. E. CASTER

1952. Geology. New York: McGraw-Hill, xii + 730 pp.

WANNER, ATREUS

1889. The discovery of fossil tracks, algae, etc., in the Triassic of York County, Pennsylvania. Pennsylvania Geol. Survey Ann. Rept. for 1887, pp. 21-35, pls. 3-13.

WANNER, H. E.

1926. Some additional faunal remains from the Trias of York County, Pennsylvania. Acad. Nat. Sci. Philadelphia Proc., vol. 78, 14 pp., pl. 3.

WOODWARD, A. S.

1907. On *Rhynchosaurus articeps* (Owen). British Assoc. Adv. Sci. Rept. for 1906, pp. 293-299, pl. 2.